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Vol. XLII *April, 1922* *No. 4*

BIOLOGICAL BULLETIN

A WEEK WITH A MINING EUMENID: AN ECOLOGICO BEHAVIOR STUDY OF THE NESTING HABITS OF ODYNERUS DORSALIS FAB.

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HABITAT.

At the edge of an extensive bottom-land farm near Lebanon, Ill., there is a large barren tract of land (Fig. 1, *B*). Its northern portion, which resembles roughly the continent of North America, is 80 feet long, 42 feet wide at its greatest breadth, and 9 feet at its narrowest. From the end that is 9 feet wide an arm 300 feet long tapers gradually until it is only 4 feet wide. In August, 1921, to the west and to the south of this desert there was a bottom-land cornfield covering several acres. The ascending slope and the upland on the east were covered with a dense growth of field sorrel, variegated with scattered iron weeds and mallow plants. On the western half of the northern boundary there was a cornfield, and on the eastern portion of that boundary there were plants similar to those on the east. Near the eastern edge of the barren tract the weeds were dwarfs, but they rapidly increased to normal size. From northeast to southwest and then south a small stream meanders through this land. The northern, especially the northeastern portion, is slightly higher and decidedly drier than the remainder. In meandering through the northeastern portion the streamlet maintains a uniform width of about six inches; in the remainder of the area it frequently widens into shallow lakelets. The flow of the water is continuous, but gentle. This apparently insignificant stream, which is the outlet of a spring with a decidedly salty taste, is the cause of all this barrenness. The minerals it conveys from that spring have destroyed the vegetation.

On the nearly level, but slightly higher, land about the headwaters of this brooklet, on the 26th of August, 1921, three colonies of *Odynerus dorsalis* were discovered (Fig. 1, *B, a, c, e*). One of these (Fig. 1, *A*) was on a spot that was absolutely barren; the other two were in spots the barrenness of which was partly interrupted by low-growing weeds (Fig. 1, *C*). At no other place in that desert strip, nor on any of the land for a half mile around, were there any colonies of this species. There, and at no other place in the neighborhood, were found the three essentials for the existence of this species: a patch of hard, dry, land, a near-by body of water, and a field infested with Hesperid caterpillars.

Evidently such a locality—a barren, or nearly barren, patch of dry, hard, ground, near-by water, accessible Hesperid larvæ—is the normal habitat of this species, for it is in just such situations that it has been found by Isely ('14, p. 282) and by the Raus ('18, p. 312). Hartman's statement ('05) that the species constructs mud nests on grass stems is the only discordant note in the literature, but his experience is radically so different from that of Isely, the Raus, and me that it is hard to believe that he is discussing the same species. Indeed, in a letter to Mr. Rau, Hartman states that it is probable that the species he discusses had been wrongly classified.

If one thinks in terms of social bees and hornets, the word populous could hardly be applied to these colonies; but they were slightly larger than those seen by Isely. Isely ('14, p. 293) writes: "*O. dorsalis* has a tendency to nest in colonies. I sometimes found an isolated nest, but usually the nests were in small groups, sometimes as many as eight. Usually only two or three wasps would share an open space in a pasture, each wasp digging one or two nests. I never found them in populous colonies like those of *O. papagorum.*" In speaking of *O. papagorum,* he says (*op. cit.,* p. 256): "Hundreds of them were at work there in the high banks of light earth." In the three colonies observed by me the number of wasps varied from twelve to sixteen. This estimate was made not by counting the wasps, but by noting the number of holes that were in process of construction or of being provisioned at the same time.

Description of the Nests.

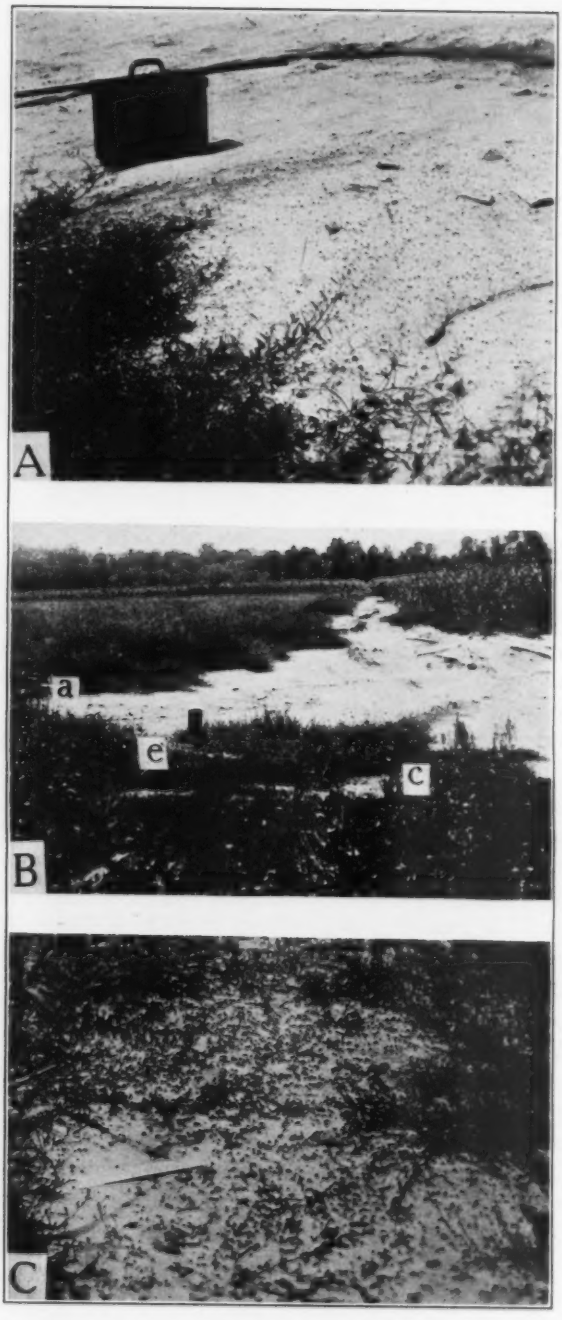
Each nest consists of one to three, usually two, barrel-shaped or sub-spherical cells for larvæ and a small air chamber, the latter being above the former. Thin partitions of clay separate the compartments from each other and a clay plug separates the whole from the outer world (Fig. 6, *B–D*). In the cases observed by me, when there were three cells, the upper was empty; when there were two cells, the upper was smaller than the lower. These nests vary in length from one and a half to two and three fourths inches. Each cell is about five eighths of an inch wide and the entrance to the nest is about three eighths of an inch. The transverse partitions are thin. Each wasp constructs a succession of nests which are arranged close together. These facts were ascertained by excavating twenty-five nests.

The above description harmonizes perfectly with Rau's observations and with the majority of Isely's; however, the latter author found some nests with as many as seven cells.

Excavating the Nest.

The nest-building behavior of these wasps is fascinating. Preliminary to digging, the wasp makes sweeping movements over about forty square inches of surface. She moves about here and there as though testing the ground. The purpose of this survey I do not know; it may be that it enables her to detect the spots where other nests are located. This surmise is supported by the fact that excavations demonstrate that the nests occur in small groups. The nests of each group are separated from one another by walls that are not very thick; yet I have never discovered one burrow running into another.

The preliminary explorations over, the wasp makes a flight of orientation and then flies to the near-by streamlet and takes a deep drink of water. Returning to the spot selected, she moistens the ground and, with her mandibles, removes several pellets of dirt and conveys them, one by one, to a distance of from two inches to two feet. She then goes for some more water and then returns to the excavating (Fig. 3, *a*). This is repeated over and over again until the lower cell has been completed and the next one partly finished.


A
a
e
c
B
C

It usually takes a little over an hour to reach this point in the digging of the burrow. In removing the dirt she goes in head first and comes out backwards.

Isely thinks that this species carries the water in her jaws. He says ('14, p. 286): "Mrs. Wasp flew in the direction of the river and returned with her mouth parts glistening." Although I watched the wasps carefully, I failed to detect water glistening on their mouth parts. However, I know that they carry water to moisten the clay; because, immediately after a wasp that has returned from the streamlet applies her head to the ground, the clay glistens for a moment and then becomes dull. The water sparkles until it is absorbed by the clay. Hence I am inclined to believe, with the Raus ('18, p. 314), that the water is carried in some part of the digestive tract (probably the crop).

In a previous paragraph I have stated that each pellet, as it is removed, is carried to a distance of from two to twenty-four inches and deposited. How carried? According to Isely ('14, p. 285), she flies and drops them all, in about the same place, at approximately eighteen inches from the nest. The Raus ('18, p. 314) write: "She would then back out of her hole with a round, well-formed pellet of mud in her mandible, always fly from two to fifteen inches and drop it." They do not state whether the pellets are scattered around or deposited in one place, but the illustration furnished pictures them distributed, in a single layer, over the ground. Of the colonies I am describing, in one (Fig. 1, *B*, *a*) the pellets were scattered, in a single layer, over the plot; in the other two, in addition to the scattered pellets, there were piles of them near certain nests. Some wasps were flying and dropping the pellets, some were walking from the nest and depositing the pellets and then flying back to the nest, some were walking from the nest, depositing the pellets, and then walking back to it. It

FIG. 1. Views of the habitat of the colonies studied. *A*. Near view of the colony located at *a* in *B*. The specks on the ground are pellets dropped by the wasps. *B*. View of the environment of the three colonies: *a*, location of a colony situated where the ground is absolutely free from vegetation; *c*, location of a colony where a few low-growing weeds partly cover the ground; *e*, a colony similar to *c*. *C*. A near view of the colony located at *c* in *B*. The specks on the ground are pellets dropped by the wasps.

was readily seen that the piles of pellets were formed by the wasps that were walking and depositing pellets. Careful observation demonstrated that the piles of pellets were always associated with those nests that were partly covered by the low weeds growing on certain portions of plots *c* and *e*. What is the cause of this striking difference in the behavior of these wasps? Are some members of the species born with an instinct for flying and scattering pellets and other members of the same species born with an instinct for walking and depositing pellets, or is there some relation between the partial covering of nests by low-growing weeds and the change from flying to walking?

Experimental Investigation of the Plasticity of the Carrying Behavior.

If some members of this species are born with an inflexible instinctive tendency to fly and scatter pellets and other members of the same species are born with a fixed instinct to walk and deposit them in piles, nothing in the way of an experiment can alter matters; but if, in response to a certain environment, the walking form of behavior has been derived from the flying, then it should be possible to experimentally demonstrate it. Since the low-growing weeds do not make flight impossible, if they are the cause of the change in behavior it must be because they render flying with a load so unpleasant that the insect takes to walking to avoid the unpleasantness. The problem that faced me was to devise some apparatus that would permit the insect to fly, but which, at the same time, would render flying with a burden so unpleasant as to cause the wasp to abandon the attempt.

In the experiments I used what might be called an interference maze, constructed out of stove wire. The maze was constructed in the field. A burrow was selected from which the wasp was flying and scattering pellets. Several pieces of wire were stuck, near together, in the ground near one of the nest openings. These wires were then so bent as to radiate over the burrow like the rays of a fan. Near the nest these wires were only an inch, or a little less, above the surface of the ground. As they extended outward they became gradually higher and higher until they

reached the point where they were bent abruptly to form a support. A series of sub-parallel, semi-elliptical wires were constructed across this fan-like expanse of wires (Fig. 2).

A number of these interference mazes were used. They were all similar, but no two were identical (Figs. 2 and 3 are from the same maze and Figs. 4 and 5 are from another). The only points invariably adhered to were two: first, in the immediate vicinity of the nest the wires were so arranged as to make it difficult for the wasp to get a flying start with her pellet of mud; second, the meshes were made sufficiently open for the wasp to fly through. Two mazes were used at a time. Each experiment extended over a period of from one to two hours. Three days were devoted to these experiments. The wasps, which invariably spent the night in the nests, became active between 7:30 and 8:00 A.M. and continued to work until about sundown. Each day the experiments were begun as soon as the wasps became active. On the first day they were continued until they became inactive; on the two other days I stopped work between four and five in the afternoon. Since two mazes were used at a time, this gave time enough for fifteen experiments.

The results of these experiments were conclusive and positive and sufficiently uniform to be epitomized in a single paragraph. In each case the wasp flew away with a few pellets (usually less than six) and then began to walk. In the midst of this uniformity there was individuality. The majority of the wasps walked from the nest, deposited the pellet (Fig. 2, *f*), and then walked back to the nest; some walked from the nest, deposited the pellet, then flew out of the maze and back to the nest. One walked to and from the pellet pile most of the time, but occasionally it would fly and scatter a pellet. Another would walk from nest to pellet pile and back until it came time to get some more water, then she would fly with the pellet out of the maze, drop it, and then go for water. Thus we have conclusive experimental proof that the walk-and-deposit-the-pellet behavior of these wasps has been derived from the fly-and-scatter-the-pellet behavior in response to an environment which made flying with a load unpleasant.

Occasionally, in arranging the maze over a certain nest, the

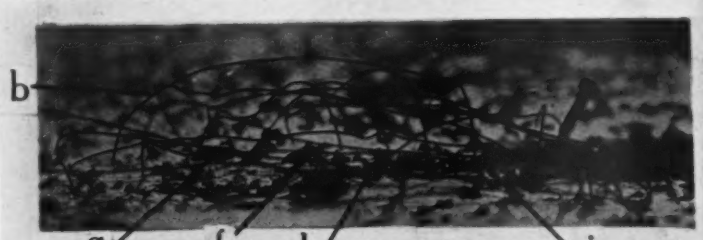


Fig. 2

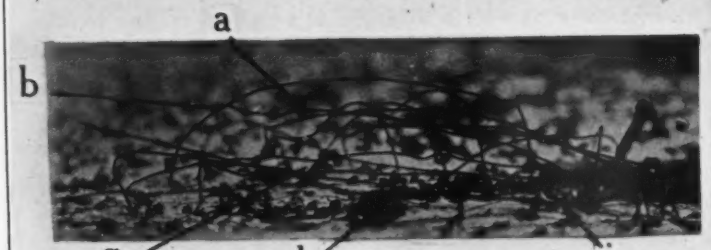


Fig. 3

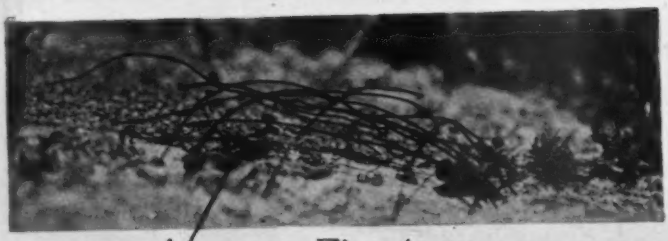


Fig. 4

Fig. 5

higher portion of the maze would cover another nest in which the wasp was still digging. In such cases the second wasp would continue to fly and scatter pellets (Fig. 4, *j*; 5, *a*). Thus, in the same maze, I sometimes had one wasp walking and depositing pellets in a pile or piles and another flying and scattering them.

It is not claimed that these experiments predicate of wasps the power of logical thinking; on that topic experiments of this type are non-committal. However, they demonstrate conclusively that, in *Odynerus dorsalis* Fab., the walking-to-deposit-the-pellet behavior is derived from the flying-to-scatter-the-pellets activity, in response to a slight change in the environment.

Experimental Interference with the Wasp When Excavating.

A series of experiments was conducted to test the reactions of excavating wasps to objects dropped into their burrows. Three kinds of objects were used in these experiments: pellets of dirt (mineral matter), short pieces of weed stems (plant matter), live caterpillars (animal matter).

Experiments with Pellets.—*Pellets of dirt that had been removed from nests by certain wasps were dropped into the partly excavated nests of other wasps.* In each case the wasp removed the pellet and disposed of it in the usual manner. In each case the return to the surface with the pellet was too quick to permit the formation of one.

Experiments with Bits of Weed Stems.—*Stems of the weed were cut into pieces about two inches long. These were placed in the partly completed burrows of the wasps. In some cases the*

Fig. 2. Showing a wasp that has been induced, by the maze, to walk and deposit her pellets: *b*, maze; *f*, wasp carrying the pellet; *g*, opening of the nest; *h*, piles of pellets deposited by the wasp; *i*, another wasp entering her nest to oviposit.

Fig. 3. Showing a wasp, that had been excavating inside the maze, flying for water: *a*, the wasp flying for water; *b*, the maze; *g*, entrance to the nest; *h*, piles of pellets deposited by the wasp; *i*, a wasp leaving her nest after depositing.

Fig. 4. Showing a wasp preparing to fly off with a pellet: *j*, getting ready for flight.

Fig. 5. Showing a wasp flying away with a pellet: *a*, a wasp flying.

nest was so shallow that only half of a wasp could be hidden in it; in others the burrow was just deep enough to include the whole of the wasp. Invariably the wasp removed the bits of weed and deposited them on the ground near by. Sometimes the wasp removed the weed stem or stems immediately; at others she continued excavating for a short time and then removed the foreign substance. It seems as though she removed the stems as soon as they greatly hampered her movements.

EXPERIMENTS WITH CATERPILLARS.—*Home-coming wasps were robbed of their prey until I had collected a dozen paralyzed caterpillars. Burrows in two stages of completion were selected: those that were just deep enough to half conceal the worker and those that were sufficiently deep to just hide the wasp. While the wasp was gone for water one of the caterpillars would be placed in the burrow and the nest watched until the wasp resumed her excavating. This was repeated over and over until the twelve caterpillars had been used.* With the exceptions of touches of individuality the behavior was invariably the same. The wasp always removed the caterpillar from the nest, flew with it to the weed-infested field, and returned empty-handed. In some cases the wasp flew away with the caterpillar as soon as arriving at the surface of the ground; more often she would climb some weed before flying away. Sometimes the journey was preceded by a longer or shorter flight of orientation, at others by none. The final flight was sometimes in one direction and sometimes in another, but always in the direction of the weed-infested field. Why did these wasps react so differently toward the several classes of objects? When pellets of earth were dropped into the nests, the wasps either flew and scattered them or walked and deposited them in piles; when short pieces of weed stems were placed in the burrows, the wasps deposited them on the ground adjacent to the nest; when paralyzed caterpillars were placed in the holes, the wasps flew with them to the insect-infested field, which was several yards away. I confess that every time a wasp flew away with a caterpillar it gave me an intellectual thrill; but, to me, the reason for the behavior remains a mystery.

Homing Experiments.

While observing these wasps excavate their nests I was deeply impressed by two things: the facility with which the wasp, on returning with water, located her nest in the midst of surroundings which, to my senses, were almost uniform, and how easily she could be confused by slight changes in the environment. Almost any disfigurement of the surface of the ground would cause her to have trouble in locating her nest. Small pieces of tile and nails used to mark certain nests and radiating lines which I scratched about others caused confusion. In each case the reaction was the same. Arriving in the vicinity of the nest, the wasp would circle about in an irregular manner, sometimes afoot and sometimes awing, as though lost. After a certain length of time it would either find the nest or else abandon the attempt and start another. If the nest were found, before taking another trip afield, the wasp would always make a careful flight of orientation.

In the following words Isely ('14, p. 294) states how easily the wasps he studied were affected by changes in the surface of the ground: "Although not generally sensitive to observation, *O. dorsalis* was more responsive to changes in the surroundings of her burrows than was *O. papagorum*. A few marks with a knife, to assist in locating a nest at a later time, seemed to disturb one wasp considerably. On her return to the nest she made a prolonged flight of irregular circles above her nest, while she was in the habit of alighting without any hesitation. On another occasion I mutilated slightly the entrance to a burrow. Upon the wasp's return she circled around the burrow a few times and then alighted about two inches from the entrance. She flew away and returned in about a minute and repeated the observation performance. Again she flew away and returned without entering. This time she apparently deserted her nest."

Evidently, when in the neighborhood of the nest, *Odynerus dorsalis* finds her way by means of landmarks. How keen, then, must be her powers of observation since she sees landmarks in a situation where we see only uniformity!

Provisioning the Nest.

The nests are stored with a black-headed, green, Hesperid larva, which the wasp obtains from the neighboring field. These are paralyzed and packed in the cell. The wasp carries the caterpillar dorsal side down and head to the front. When she reaches the burrow she pushes the caterpillar in ahead of her. Sometimes at one stage and sometimes at another in the provisioning of the nest the wasp folds her wings close to the body and backs into the nest (Fig. 2, *i*), attaches her egg to the roof of the cell by means of a cord about as long as the egg, and then comes out head first (Fig. 3, *i*) and resumes her work. This statement is an assumption based on the following facts: There is never found more than one egg suspended from the top of a cell; only once during the provisioning of the cell does the wasp back in; the attitude attained by backing into the cell is the most favorable one for attaching the egg to the roof. When this lower cell has been filled, the wasp fetches some water and then, out of the scrapings from the walls of what is to be the next cell, she covers the first with a clay wall. In most cases, after this partition has been formed, the second cell is the right size for receiving the provisions; occasionally the wasp must remove a few pellets before storing it with caterpillars. After it has been provisioned a mud cover is made for it out of scrapings from the wall of the upper portion of the burrow. The burrow is then closed with a plug of mud and dirt. The material to form this plug is scraped from the rim of the burrow; as a result the freshly formed burrow is topped with a saucer-like depression. After a few days, or even a few hours, the wind, the rain, and the pellet-dropping activities of other wasps obliterate the depression. To obtain sufficient water for the softening of the clay the wasp makes frequent trips to the near-by streamlet. During the whole time that the provisioning is progressing the burrow remains wide open. The above account tallies with those of Isely ('14, pp. 289–290) and the Raus ('18, p. 320).

Experimental Interference with the Provisioning Activities of Wasps.

While the wasp was in the nest arranging her provisions from one to four caterpillars were dropped into the burrow. Some of

these larvæ were obtained by robbing home-coming wasps; the majority were obtained by excavating nests that had been stored and sealed. Fifteen such experiments were performed. On one occasion, when I had dropped two caterpillars into a nest, the wasp left the burrow and went hunting without removing them. Later in the day she took two caterpillars from her nest and carried them to the field; but there is no way of telling if these were the two added. On another occasion, when three caterpillars had been dropped into a nest and two deposited on the ground near the nest, the wasp, on emerging, captured one of the caterpillars that had been placed on the ground near the nest, flew with it to a near-by weed, stung it, malaxated it, and then carried it into the burrow. Immediately she emerged with a caterpillar and flew with it to the near-by field. She then continued to remove caterpillars from the nest until she had conveyed five to the field. In all other cases the wasp carried the caterpillars afield as soon as they had been dropped into the nest. It seems that the wasp is averse to using caterpillars that have been captured by some other wasp, and that she has some means of distinguishing them.

To see if she could recognize her own captures, I frequently removed the prey from a home-coming wasp and dropped it on the ground among the nests. Invariably she would search until she found the caterpillar and then would carry it to her nest.

With a pair of forceps I occasionally attempted to remove the caterpillar from a wasp that was walking on the ground near her nest. She would make strenuous efforts to retain her hold, occasionally stinging the larva. If I succeeded in removing the caterpillar, the wasp would search for it until found and then store it in her nest.

Isely ('14, p. 294) states: "*O. dorsalis* never seems to have any difficulty in finding her way to her burrow after a field trip. Usually she flies directly to it; I never saw her do otherwise when she was returning from the field with prey. At times, when she returned from the field unladen, I have seen her pause at another burrow in the colony. This action may have been prompted by curiosity instead of being a mistake in location." In that same connection the Raus write ('18, p. 320): "These wasps, when re-

turning from the field, seem to experience no difficulty whatever in locating their burrows. They carry their prey on the wing, usually with comparative ease, hugging it tightly all the while, alight at the brink of the hole and push it in ahead of them, holding it as they lower it; then they follow it into the hole, remain inside a few seconds—perhaps a half minute—and then come backing out. Sometimes the wasp soars away directly in quest of other game; at other times she sits down and washes her face for a moment, then rises and poises on vibrating wings an inch or two above the hole, turns around on the wing as if inspecting the site, then circles about and flies away. She is calm, gentle, and composed in all the maneuvers, betrays no nervousness, and wastes no time in blustering." Since I had read both of these accounts before making my observations on the same species, I was surprised to find that wasps coming from the field did sometimes have difficulty in finding their nests. My wasps, when arriving laden from the field, sometimes went direct to the nest and pushed the caterpillar in; but usually they did not. Frequently a wasp would examine the entrances to several nests before entering one. At other times a wasp afoot and awing would circle around and around for several minutes before entering the nest.

Movements as conspicuous as these, if performed by the wasps they studied, could not have been overlooked by such keen observers as Isely and the Raus. Why should my wasps behave so differently in this respect? I think I have the solution. In arranging mazes for experimental work, and in marking certain nests with bits of tile and with nails, I was continually disfiguring the ground. Since my wasps spent from ten minutes to more than half an hour on each hunting trip, it is quite likely that during the absence of a wasp the ground would be changed sufficiently to confuse her. A careful consideration of the records of my first afternoon's work confirms this opinion. Then the ground had not been disfigured with pieces of apparatus. To see if the colony was worth careful study, I made a few observations and marked a few nests. In most of the records of that afternoon the caterpillar-bearing wasps are described as going direct to their nests. Two records tell a different story and those two were connected with

nests that had been marked. I shall transcribe both of those records, because they have a direct bearing on this point. We shall call them records of wasp *A* and *B*.

Record of wasp A:

11:20 A.M. The wasp places a caterpillar in the nest and departs for the field. *I place a small piece of tile near the opening.*

11:30 A.M. The wasp returns with a caterpillar. She does not recognize the nest. She spends thirty minutes returning over and over to the same spot, but fails to recognize the nest.

12:12 P.M. *I remove the piece of tile.* Within two minutes the caterpillar is carried into the nest.

Record of wasp B:

11:34 A.M. The wasp carries the caterpillar into the nest, makes a flight of orientation, and then flies afield. *I place a small piece of coal to mark the nest.*

11:44. The wasp returns with another caterpillar, goes to the wrong hole, and, still bearing the caterpillar, flies about in irregular curves.

11:45. The wasp starts into the hole, leaves it and tries another. Still bearing the caterpillar, she flies about.

11:58. The wasp deposits the caterpillar in the nest and goes for water.

11:59. The wasp returns and begins to scrape the rim of the burrow and to add the material to the inside of the nest.

Evidently the wasp when returning with a caterpillar is just as sensitive to changes in her environment as she is when excavating.

I have a very strong suspicion, but not positive proof, that these wasps sometimes carry the caterpillar into the wrong nest. Occasionally I have seen a wasp, belonging to some nest upon which I had not experimented, remove a caterpillar and fly with it to the field. The Raus ('18, p. 324) have noticed the same thing. They write ('18, p. 324): "From one hole we saw an *O. dorsalis* emerging and watched her closely to ascertain her method of egress. Imagine our surprise when we saw her carry out a *P. catullus* caterpillar in her front and middle pair of legs, pause at the brink of the hole for several seconds to adjust the caterpillar properly between her forelegs and mandibles, and fly away with it." The

behavior of these wasps is identical with that of those into whose nests I had introduced caterpillars that had been captured by other wasps. It seems reasonable to assume that these caterpillars have been deposited in the nest by some other wasp.

Time Required to Provision the Nest.

Isely found ('14) that many of the specimens examined by him excavated, provisioned, and sealed the burrows in less than two hours, although some of the individuals took a day for the work. In every case that I followed from beginning to the end the wasp always constructed the burrow one day and sealed it on the afternoon of the next day or the morning of the day after. Thus the time elapsing from the beginning of the excavation to the final sealing of the nest was twenty-four hours or more. Since the amount of time consumed in excavating the burrow was about the same in each case, the greater length of time required by my wasps to complete the work may have been due to lack of food. Isely's colonies were located where the mallow was abundant; my wasps were situated near a large field of field sorrel, scattered through which were a few mallow plants. On one occasion I followed a wasp, from plant to plant, for more than half an hour. She examined leaf after leaf, without finding any caterpillars. I uncoiled several leaves, but found them empty.

Capturing the Prey.

Isely ('14, p. 289) writes as follows: "When *O. dorsalis* would come upon a crumpled leaf containing the larva of the spotted skipper, she would commence tearing energetically at the silken nest, first at one end and then at the other. Although the wasp worked furiously and without pausing, sometimes more than five minutes were required to dislodge the caterpillar. Usually, however, in less than a minute the caterpillar would be jerked violently from the cover, seized by the neck, and stung two or three times under the thorax. Once I saw a wasp seize a caterpillar by the tip of the abdomen, to jerk it out of the nest, and sting it under the last abdominal segments. Then she quickly seized the neck and gave it three thrusts under the thorax. A vigorous malaxation

invariably followed the stinging. The capture of a caterpillar usually caused considerable excitement on the part of the wasp. Sometimes she would lose her footing and both insects would roll from the leaf to the ground before the victim could be subdued."

Although I have watched this wasp searching the crumpled leaves for caterpillars, I have never been on hand at the moment she captured her prey. However, I have witnessed both the stinging and the malaxation of the victim. The first time I noticed the malaxation the wasp and the caterpillar were on the leaf of a weed and the wasp was vigorously crushing the neck of the larva with her jaws. Then the body of the caterpillar was moved forward until every portion of the body had been crushed by the rapidly moving mandibles. I witnessed the stinging on two occasions. Once a wasp captured a paralyzed caterpillar which I had placed on the ground near her nest. The larva was seized by the neck, the abdomen of the wasp curved beneath the caterpillar, and the sting of the wasp thrust into the thorax three times. On another occasion, by means of forceps, I was attempting to pull a larva away from a wasp. Suddenly she stung the caterpillar three or four times. These thrusts were in the front part of the abdomen. The stinging and the malaxation do not kill the caterpillars, but leave them in a semi-paralyzed condition. In all of the nests that I opened, if they contained eggs or young larvæ, the caterpillars squirmed when exposed to air.

Visitors to the Colony.

During my week's sojourn with these wasps several species of insects visited the colony. A large species of assassin fly occasionally visited the scene. She would rest quietly on the ground in the midst of the colony and make her toilet. When a wasp approached she would become as rigid as a stone; but never did I see her make an attempt to capture one of the wasps.

Two species of dipterous parasites appeared. One fly (probably a species of *Hilarella*[1]) occasionally followed a laden wasp in

[1] The scientific names of all the visitors are not given; because, when they were common, the experiments required so much of my time that I could not capture them. On the afternoon that I set aside for capturing them no visitors appeared.

from her hunt. Just before the wasp entered the nest she made movements as though attempting to oviposit on the caterpillar. Another parasitic fly occasionally rested on the ground at the mouth of a nest from the time the wasp entered with a caterpillar until she emerged. She would then enter the nest, remain a short time, and then leave.

In excavating the nests of this species the burrows of two more mining Hymenoptera were found. One of the nests (Fig. 6, *A*)

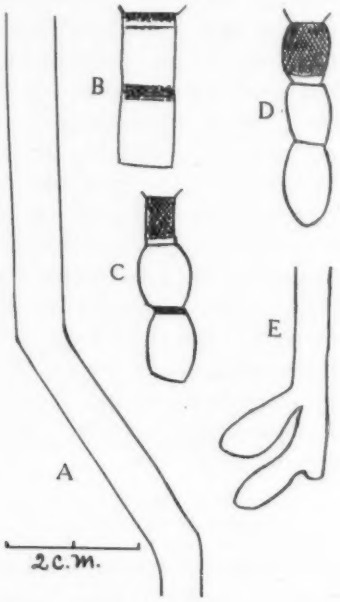


FIG. 6. Nests of certain wasps.
A, Burrow of *Cerceris* sp.? [Unfinished.]
B–D, nests of *Odynerus dorsalis* Fabr.
E, Burrow of an unknown visitor.

is an incompleted burrow of *Cerceris* sp.? I saw the wasp leave this nest. The other (Fig. 6, *E*) had a long vertical burrow; near the bottom of the shaft, on one side, were two cells. These cells made an angle of about forty-five degrees with the central shaft.

Conclusions.

1. The habitat of *Odynerus dorsalis* is a level, or practically level, tract of barren or almost barren land situated conveniently to a supply of water and of Hesperid caterpillars.

2. The nests are constructed in the ground; they are vertical and consist of one to three, usually two, cells, which are separated from each other by clay partitions. In rare cases the number of cells may be larger than this.

3. They occur in colonies of moderate size.

4. In order to work the clay it is wet with water obtained by the wasp from some near-by stream, or pond, or puddle.

5. In excavating the nest the wasp works the soil into balls and carries it out of the nest. Normally she flies with the pellet to a distance of from two to twenty-four inches, but if overhanging vegetation or other impediment renders flying with a burden unpleasant, she walks and deposits the pellets in one or more piles.

6. During the periods of excavating and of storing the nest the wasp is guided by landmarks; this is evidenced by the fact that any changes in the surface of the ground always serve to make it difficult for her to locate the nest.

7. The eggs are attached to the roof of the cell by means of a short thread. There seems to be no definite stage in the provisioning of the nest for the oviposition. At that time the wasp backs into the cell to lay and then walks out head first.

8. The Hesperid caterpillars with which she stores her nest are packed in until the cell is full. Since the cells are not all of the same size, the number of caterpillars in the cells varies. In all of the nests examined by me the lower cell is the larger.

9. In all of the cells examined by me the caterpillars were active enough to squirm when exposed to the light and the air.

10. If, during her absence to get water, pellets of mud or bits of weed stems are dropped into her nest, the wasp, on returning, removes them and deposits them on the ground near the nest. If paralyzed caterpillars are dropped into such a nest, under the same conditions, the wasp will fly with them to a distance of several yards.

11. If caterpillars captured by another wasp of the same species

are deposited in nests of wasps that are provisioning their nests, they will be removed and carried to a distance of several yards.

12. When slight changes are made in the surface of the ground near the nest, wasps returning home laden with caterpillars have difficulty in finding their homes, and sometimes enter the nests of other wasps.

13. In the midst of a colony of these wasps other mining Hymenoptera sometimes establish burrows.

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THE COLONY FOUNDING OF *ACANTHOMYOPS (DENDROLASIUS) FULIGINOSUS* LATR.

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Mons. R. Stumper ('20), having recently recorded the discovery of three isolated *fuliginosus* females in cells under stones, considers that these facts alone diminish the probability that the manner of starting colonies adopted by the *fuliginosus* is the dependent one, and that further investigation may prove this. We are personally of the opinion that the colony-founding habits of this ant are now well known and thoroughly established, not only by discoveries in the field, but by exhaustive experiments carried out in the laboratory. We propose to review the entire evidence on the subject in the order of date on which the various records and discoveries have been made; and to deal, therefore, with Mons. Stumper's remarks at the end of the paper.

Donisthorpe ('97) records that he found at Lymington a large colony of *A.* (*D.*) *fuliginosus* nesting in a hollow tree, and that a colony of *A.* (*Chthonolasius*) *flavus* was living in the same nest, both species coming in and going out together. With our present knowledge we know that it would be impossible for *fuliginosus* and *flavus* to live together, and that instead of the latter ant the species must have been *umbratus* or *mixtus*.

De Lannoy ('08) writes that in 1904 he found at Knoche-sur-Mèr in Belgium a few workers of *mixtus* living in a large colony of *fuliginosus*, and in 1906 he again found several similar colonies. He suggested as an explanation that the *fuliginosus* had stolen the larvæ and pupæ from a colony of *mixtus* which they had attacked, and that a few of the latter's brood, which had not been devoured, had been reared in the nest of the former ant.

Forel ('08) and Emery ('08), when commenting on de Lannoy's suggestion, expressed the view that it was a case similar to those in the *Formica* groups where the females have lost the power of founding their colonies unaided, and that a female *fuliginosus*

after the marriage flight had been accepted into a nest of *mixtus*. After the natural or violent death of the *mixtus* queen, the brood of the *fuliginosus* queen had been brought up by the *mixtus* workers; the black ants gradually increasing and the yellow dying off little by little, until eventually a pure black colony was left.

Wasmann ('09) called attention to the ability of *fuliginosus* to form new colonies by sending off detachments of queens and workers after the manner of *Formica rufa*. He further accepted the interpretation given by Forel and Emery of de Lannoy's discoveries, and recalled the fact that he had himself on several occasions found mixed colonies of *fuliginosus* and *umbratus*. He hoped that future experiment would clear the matter up.

Crawley ('10) records that in 1898 he frequently found workers of a large bright yellow ant among the workers of a *fuliginosus* colony nesting in his house near Oxford. He thought at the time that the yellow individuals were workers of *flavus*, but is now satisfied that they were *umbratus*.

Donisthorpe ('10) points out that colonies of *fuliginosus* are often numerous in a district in which it occurs, and that it partly founds its colonies by branch nests. He mentions that Wasmann had frequently found *umbratus* nests at the foot of trees inhabited by *fuliginosus*, and that the queen of the latter had probably founded her colony in the nest of the former. He refers to Crawley's record of *umbratus* workers in a *fuliginosus* nest and to his own of 1897. He says he is now convinced that the species was really *umbratus;* he was not so well acquainted with our ants at the time, but he remembers distinctly thinking how large the "*flavus*" were.

Wheeler ('10), when describing an aberrant *Lasius* from Japan, discusses thoroughly the colony founding of *fuliginosus*. He writes: "Unlike the queens of the common *Lasius niger*, the queen of *fuliginosus*, after fecundation on her marriage flight, and on returning to the earth, is unable to start a colony unaided, and if prevented from rejoining the maternal colony, or a detachment of workers of her own species, has to seek out a colony of *L. umbratus* and have her young brought up by the workers of this ant. The *umbratus* queen must be killed either by her own workers or by the intrusive *fuliginosus* queen, so that the host species is destined

eventually to die off and leave a pure and thriving *fuliginosus* colony." That this method of colony founding is actually adopted by *fuliginosus* queens is clearly indicated by the following observations which have been slowly accumulating during the past few years. He then proceeds to review the writings of Crawley, Donisthorpe, Emery, Forel, de Lannoy, and Wasmann; and gives some further illuminating and interesting remarks on the genus *Acanthomyops* (*Lasius*).

Donisthorpe ('11*a*), in a paper read before the Entomological Society of London on December 7, 1910, mentions briefly all that was known to date on the colony founding of *fuliginosus*, referring to the writings and views of all the above-mentioned myrmecologists. He further says that a worker of *umbratus* had been sent to him to name on September 20, 1900, by a Mr. Tuck, who had taken it in a *fuliginosus* nest situated in a horse-chestnut stump at Bury St. Edmunds. He then stated: "My friend Mr. Crawley and I intend to carry out experiments with *fuliginosus* queens and observation nests of *umbratus* next year."

Donisthorpe and Crawley ('11*b*), in a paper read before the Entomological Society of London on November 15, gave the results of the above-promised experiments, which they published in detail. These experiments were entirely successful, and proved without doubt that a female *fuliginosus* will be accepted and her brood be brought up by the *umbratus* workers. They reviewed all the previous discoveries and gave a complete list of the literature on the subject.

The same two authors ('13), in a voluminous paper on the founding of colonies by queen ants read at the Second International Congress of Entomology held at Oxford in 1912, gave a very complete account of the colony founding of this ant, including all experiments and discoveries, in detail, made up to date.

Donisthorpe ('13), in a paper on some remarkable associations between ants of different species read before the Lancashire and Cheshire Entomological Society, briefly referred to the colony founding of *fuliginosus* queens in nests of *umbratus* and *mixtus*.

Donisthorpe ('15*a*), in his book on "British Ants," gives a full account of the colony founding of this species. It seems as well to reproduce the whole of this account here, as it gives the main

facts of the experiments by Crawley and himself referred to above (which would have taken up too much space to give in detail in this paper), and records further experiments. "Crawley and I have shown that the female (*fuliginosus*) does not lay till the year after impregnation, and we have proved her to be a temporary social parasite, as will shortly be seen. . . . *D. fuliginosa* often founds new colonies by branch nests, which accounts for the fact that many colonies are found in the districts where this ant occurs. After the marriage flight newly fertilized females are received back into the parent and other *fuliginosa* nests near by. Occasionally, however, deälated females are found wandering about in localities some distance from their nests. Forel records finding a number of deälated females on roads at Soleure on July 21, 1869, and Crawley found one at Oddington, near Oxford, about one hundred yards from a nest, and others at Esher in August, 1899, and in such cases as these the females would not be likely to be received back into their own nests. However, when isolated they display no desire to found a colony. Crawley and I have both kept in captivity newly fertilized females which get rid of their wings immediately after impregnation; and they never settle down, but endeavor to escape, and soon perish.

"Therefore, from the above facts alone, it seems doubtful whether the female of this species can found a colony unaided. But further observations in the field point to *umbratus* and *mixtus* as the host species of *fuliginosus*. In 1897 I found at Lymington a large colony of *fuliginosus* in a hollow tree, and *umbratus* was undoubtedly living with it, as workers of both species were going in and out of the same holes. Crawley in 1898 repeatedly found workers of *umbratus* walking unmolested with the workers of a large nest of *fuliginosus* established under his house near Oxford. In September, 1900, Tuck sent to me a worker of *umbratus* taken in a nest of *fuliginosus* at Bury St. Edmunds. In 1904 de Lannoy found at Knoche-sur-Mèr a few workers of *mixtus* in the midst of a large colony of *fuliginosus* which were on good terms with the workers of the latter, and in 1906 he again found workers of *mixtus* in several *fuliginosus* nests. Forel, Emery, Wasmann, Wheeler, and I commented on de Lannoy's observations, and expressed the opinion that the presence of these *mixtus* workers was

due to the fact that fertile *fuliginosus* females had entered nests of the former species and been accepted. The queens of the *mixtus* had then died, or had been killed, either by their own workers or by the *fuliginosus* females, and the offspring of the latter were reared by the *mixtus* workers. In the course of time many of the latter had died off, and the few found in the nests were the survivors of the original *mixtus* colonies.

"Crawley and I determined to test this hypothesis by experiments on captive colonies. In July, 1910, a portion of a nest of *fuliginosus* was dug up at Darenth Wood, containing a quantity of workers, larvæ, males, and winged females, but no queen. The ants and brood were divided into two equal portions and each established in a four-chambered 'Janet' nest. (It may be here mentioned that this ant can not be kept in close confinement, but that if an observation nest be connected by long glass or india-rubber tubes to another plaster nest, or glass bowl, or some other contrivance in which their food is placed, the ants will thus obtain sufficient exercise.) During July all the males died and most of the females, with the exception of about twelve, which were found to be deälated. As some of these latter subsequently laid eggs, from which larvæ were reared, it is highly probable that mating had taken place inside the nests.

"In the beginning of December, 1910, a nest of *umbratus* without a queen was obtained at Weybridge and divided into two equal portions, which were established in 'Janet' nests. The first experiment was made on December 10, when one of the deälated female *fuliginosus* was placed in the light chamber of one of the *umbratus* nests. She immediately entered the most crowded chamber; one worker saluted her and another dragged her further by a mandible, but eventually she was attacked and killed before evening. On December 13 another deälated female was put into a small plaster nest with some of the workers from the same *umbratus* nest as in the former experiment. She was slightly attacked, but made no resistance, and endeavored to conciliate her assailants by stroking them with her antennæ. When a worker endeavors to bite at the waist of one of these females, she protects it by crossing her hind legs over her back, and when at the neck by pressing her head back close against the thorax. A few more workers were added,

and on December 20 she was introduced with the workers into the *umbratus* nest. She was a little attacked by workers who had not seen her before, but the old workers protected her, getting between her and the others, and pulling them away by the leg, but very soon all hostility ceased, and she was evidently accepted. Many workers surrounded her, caressed and fed her, and all went well till April, when, a number of the workers having died off, some four hundred more were obtained from the Weybridge nest and introduced. These newcomers attacked the queen, though they were quite friendly with their sister workers, and as they persistently refused to accept her, she was removed and returned to her own nest on April 21. The *fuliginosus* workers were very excited at her appearance in their nest, and she was much pulled about, but eventually lost sight of amongst the crowds of ants. On July 23 a female with her gaster enormously dilated was noticed in the *fuliginosus* nest, with a large pile of eggs and surrounded by workers, which may possibly have been the female of the above experiment. In the next experiment a female *fuliginosus* was still more easily received into the other *umbratus* nest, and by December 16 she was completely accepted. On March 22, 1911, another *fuliginosus* was introduced into this nest and was immediately accepted without any hostility whatever, as was the case with two more which were introduced in April, but subsequently removed. The two queens first introduced in this experiment began to lay on March 17, 1911, for the first time, and these eggs hatched on August 9. In 1912 they began to lay on June 29, and laid more eggs than during the previous year, but nothing came of these. Some of the larvæ which hatched in August, 1911, were nearly full grown in the summer of 1912, but they remained in this condition until 1914. A larva first pupated on June 23, 1914, and several more subsequently, but none of them reached the perfect state. As these were from eggs laid in May, 1911, it will be seen that they took over three years to develop as far as the pupal stage!

"In 1913 I made a similar experiment with a nest of *mixto-umbratus* obtained at Weybridge on August 11, 1912, and subsequently strengthened with workers of *umbratus* from Wellington College. On September 14, 1913, two fertilized females, from the Oxshott nest before mentioned which had just removed their

wings, were introduced into the *mixto-umbratus* nest, when they were very little attacked and completely accepted the same day. The one died on October 12, but the other has been treated by the workers as their queen, having been fed, cleaned, and caressed by them, and is still alive in this nest—she laid her first eggs on July 12, 1914. As the females of *fuliginosus* are only slightly larger than the workers, and as their fertility is delayed for so long a period, it is clear that they are unable to found colonies unaided; they are hyper-temporary social parasites, since, as will be seen presently, *umbratus* and *mixtus* are temporary social parasites of *niger* and *alienus*."

Donisthorpe ('15*b*) recorded the death on August 29, 1915, of the above-mentioned *fuliginosus* queen which had been accepted on August 11, 1912, into a colony of *mixto-umbratus*. The workers in this nest had all gradually died off, and a large number of fresh *umbratus* workers were obtained from Woking and put into the nest. These accepted the old *fuliginosus* female at once. She was very weak and died a few days afterwards, but not from injuries. The workers had never shown any animosity toward her, treating her from the first as their queen.

Donisthorpe ('16), having been left with the above-mentioned queenless *umbratus* nest, obtained a number of virgin *fuliginosus* females from a colony of that ant nesting in the ground under a broom bush at Weybridge. On September 3, 1915, he removed the wings from one of these females and introduced her into the observation nest containing the *umbratus* workers. She ran about among the *umbratus* workers, tapping them with her antennæ; she was not attacked and soon gained the last (dark, damp) chamber of the nest, which contained the bulk of the *umbratus*. She appeared to have been accepted at once and was saluted, cleaned, and fed by some of the workers. She was treated as their queen, and was not attacked until September 7, when, the nest having been left in the sun, some of the workers began to attack her and pull her about. The nest was placed in a cool, dark place, and by September 19 she was once more thoroughly accepted as queen; she has not been attacked since, and on December 19 she was surrounded by a large court of attendant ants. Wheeler first demonstrated that if the wings be removed from a virgin *Formica* female

it causes her to behave as would a fertilized one. I have subsequently found this to be the case in all such experiments with *Formica* females. In the genus *Acanthomyops,* Crawley has recorded that the act of removing the wings from virgin *umbratus* females was far from arousing the instincts possessed by a fertilized queen. In the above-mentioned experiment with a virgin female of *fuliginosus,* however, the effect caused by removing the wings was to make her act undoubtedly as would a fertilized queen.

Donisthorpe ('17) continues the story of the virgin *fuliginosus* female mentioned above. By April 22, 1916, her gaster had commenced to swell, and on May 25 she laid a few eggs. On June 9 a larger packet of eggs was present, held up in one mass by several of the *umbratus* workers. On June 25 two larvæ had hatched, the eggs having taken over two months to develop. The eggs continued to hatch very slowly, and on November 28 some fifteen small larvæ were present. On January 28, 1917, ten medium-sized larvæ were counted, and the *fuliginosus* female was surrounded by a number of the *umbratus* workers.

Donisthorpe ('18) reports further concerning this *fuliginosus* female. On May 1, 1917, a fresh packet of eggs had been laid and the gaster of the female was considerably swollen. On May 22 there were present over 200 *umbratus* workers, the *fuliginosus* female, one packet of eggs, and 9 full-grown larvæ. May 24 some of the *umbratus* workers were covering the larvæ with bits of plaster, etc., to help them to spin their cocoons. Unfortunately during the author's absence in June and July the nest was allowed to get too dry, and on his return he found the eggs, larvæ, and pupæ had disappeared, and most of the *umbratus* workers had died. On August 18 a number of *Acanthomyops* (*Donisthorpea*) *niger* worker cocoons from Woking were introduced, and these were collected by the few remaining *umbratus* workers. The workers from the *niger* cocoons began to appear on August 26, and by October 13 all had emerged and were surrounding the *fuliginosus* queen. A number of fresh *umbratus* workers were brought home from Weybridge on October 16 and a few at a time were introduced into the nest to strengthen the colony. At first the *niger* workers killed them, and this went on till November, when a few were received. From then onwards four, five, and six *um-*

bratus workers were added every day, the *niger* workers no longer attacking them; neither did they attack the *niger* workers, nor the *fuliginosus* queen. The latter began to swell with eggs again on November 20. On December 31, 1917, there were present 60 *niger* workers and a large number of *umbratus* workers; the latter now surrounding the *fuliginosus* queen.

Donisthorpe ('19) mentions that in 1918 the *umbratus* workers in the above-mentioned nest started to kill the *niger* workers, all having been killed by May 17, 1918, when only one remained, which was killed before the end of the month. The *fuliginosus* queen gradually got very swollen again, and by May 27 she had laid a small bunch of eggs, which was held up by several *umbratus* workers. On June 16 two packets of eggs were present, but they were all eventually devoured by the *umbratus* workers. (The following is extracted from my notebook and has not been published before. The virgin female *fuliginosus* died in May, 1919, having lived in captivity for nearly four years. On April 25, 1919, she was very swollen with eggs, but almost dead, being held up by a number of the *umbratus* workers; and on May 1 she was quite dead, but still carried about by the workers until May 17, when her body was cut up. The *umbratus* workers then commenced to die off, so they were turned loose in the garden in June.) He further records that on July 17, 1918, he discovered in the New Forest a very interesting mixed colony of *A.* (*D.*) *fuliginosus* and *A.* (*C.*) *mixtus*, which consisted of about two thirds of the former workers to one third of the latter. The two species were walking along together in files on a fence near a railway bridge; they were quite friendly, tapping antennæ and saluting each other when they met on the tracks, as also when placed together in a small tube. The tracks led right down the brickwork of the bridge to the ground beside the line. It was really a beautiful sight, when the sun was shining, to see the jet black *fuliginosus* and yellow *mixtus* marching in files up and down the wall of the bridge and saluting each other when they met. As *mixtus* is very subterranean in its habits, it must have learned from the *fuliginosus* to march in files in the open. The tracks also led to and from a thick bramble grove growing by the side of a fence along the buttress of the bridge, and here the nest was evidently situated. He pointed out

that here was a case where a *fuliginosus* female had evidently founded her colony in a nest of *mixtus*.

On May 29, 1919, Mr. H. M. Hallett discovered a mixed colony of *fuliginosus* and *mixtus* in a wood at Cwrt-yr-ala in Glamorganshire. The shoots from the stump of a felled oak were covered with Aphides, and all over the stump and shoots numbers of *fuliginosus* and *mixtus* workers occurred together. They were in the proportion of about 6 to 4.

Stumper ('20) briefly refers to de Lannoy's records and the views held on the subject by Emery, Forel, and Wasmann. He considers that three, in particular two, discoveries he made in the summer of 1917 at Neuenstadt speak against the general validity of their opinions. There he found two isolated *fuliginosus* queens "in their cells," situated under stones; but no brood was present. The third was under a stone which covered a nest of *mixtus*, but "her cell" did not communicate with the galleries of the latter. It will be seen that his knowledge of the literature on the subject does not appear to extend beyond 1909—at any rate, he entirely ignores everything that has been written by Crawley, Donisthorpe, and Wheeler! His latest discovery, of course, really confirms the fact that *fuliginosus* females found their colonies in *mixtus* nests. The female in question was no doubt only waiting for a suitable opportunity to enter the *mixtus* nest. She was probably "in quarantine," for the same reason that beetles of the genus *Atemeles* hang about a nest of *Formica* before they enter it after leaving one of *Myrmica*. It is only in observation nests that a *fuliginosus* queen has to put up with such a severe test as going straight into a nest of the host species from her own. After fertilization, should a female not be able to return to the parent colony, or enter a nest of another colony of the same species, she would have to wander about in search of a *mixtus* or *umbratus* nest, and would naturally hang about near by after she had discovered it. She would not only thus lose her own nest "aura," but in part acquire that of the other. As to Stumper's two first instances, it is possible that there may have been colonies of *umbratus* or *mixtus* in the near vicinity. Or after hunting about in vain for such these females may have crept under stones for shelter. It is not to be supposed that every female who finds herself stranded is successful in her

search for colonies of her hosts. Finally, as we have already shown, *fuliginosus* females are not much larger than their workers, and do not possess large gasters supplied with plenty of fat to enable them to bring up their brood unaided, especially taking into consideration their long-delayed fertility. *Moreover, it has also been proved by experiment that they are unable to do so!*

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OBSERVATIONS ON GIGANTIOPS DESTRUCTOR FABRICIUS AND OTHER LEAPING ANTS.[1]

WILLIAM MORTON WHEELER.

In any study of the very exuberant ant-fauna of the Neotropical Region one can not fail to be impressed by the striking contrast between certain genera like *Eciton, Pseudomyrma, Solenopsis, Crematogaster, Cryptocercus, Azteca,* and *Camponotus,* each represented by a large number of variable species, and genera like *Paraponera, Acanthognathus, Daceton, Blepharidatta, Stegomyrmex,* and *Gigantiops,* each represented by a single, very stable species. Of course, such monotypic groups may be regarded either as very ancient, embracing during some former age many species of which only one has survived, or as single species which, after acquiring generic status in the remote past, have since undergone little or no modification. The individuals of a species representing a monotypic genus may be either very rare or local, mere relicts of a bygone age, or prominent and ubiquitous over larger geographical areas. This is true of such ants as *Paraponera clavata* Fabr. and *Gigantiops destructor,* which I have recently had abundant opportunity to study in the jungle about the Tropical Laboratory of the New York Zoölogical Society at Kartabo, British Guiana. As the latter species is the more imperfectly known, I have singled it out for special consideration.

The name *Gigantiops destructor* conjures up visions of a huge-eyed, insatiable monster, a kind of Cyclopean insect-jaguar. Fabricius, when he first described the insect in 1804 as *Formica destructor,* certainly knew nothing of its behavior and probably gave it what seemed to him an appropriate specific name for any ant measuring a centimeter in length. More than half a century later ('58) Frederick Smith received specimens taken by Bates at Ega, Brazil, and believed them to represent a new species which he described as *Formica solitaria.* The following note was appended

[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 177.

to the description: "This is a very remarkable insect; for independent of the enormously developed eyes and produced clypeus, the palpi are elongated to half the length of the thorax, the maxillary are six-, and the labial four-jointed. Mr. Bates says: "This curious solitary ant is never seen by more than one at a time, prowling about fallen leaves, etc., in the forest; I have never seen its formicarium and, from its solitary habits, have no clue to guide me in looking for it." Perhaps Smith was confirmed in his choice of the specific name by the monastic or ascetic appearance of the insect, its somber black livery, relieved only by the golden-yellow tips of its antennæ, its long, emaciated limbs and its huge eyes, perpetually dilated as if in astonishment and chagrin at the indecent behavior of other insects.

Two short notes, however, by later observers indicate that *Gigantiops* may be neither an insatiable assassin nor a humble anchorite, but a harmless and perhaps rather frivolous creature, that may have become permanently goggle-eyed through an age-long endeavor to enjoy to the full the riotous beauties of its environment. Emery ('93) was informed by Albert Schulz that the "Brazilian ant, *Gigantiops destructor* Fabr., which is distinguished by its enormous eyes, leaps from twig to twig, like the *Odontomachus hæmatodes* living in the same places," and Mann (1916) says: "In life this is one of the most attractive ants encountered. It lives always in the forest, where it forages either among the branches of trees or on the ground. The movements of the foraging worker are rapid, comparable to some of our species of *Cicindela*, and the bicolored antennæ are kept constantly in motion."

Roger ('63) was the first to throw Smith's *Formica solitaria* into the synonymy and to establish the peculiar genus *Gigantiops*. In more recent myrmecological literature mention of the insect recurs sporadically and at long intervals, showing that it was rarely seen in the many collections of South American ants examined by Mayr, Forel, Emery, Santschi, and others. Its known range, as indicated by the literature and by specimens in my collection, is as follows:

Brazil: Ega (Bates); Pará (E. Goeldi, ex coll. Forel); Maranhao (Ducke); Pará, Abuná, Porto Velho, and Madeira-Mamoré R. R. (W. M. Mann).

French Guiana (Jelski).

British Guiana: Kaieteur Falls, Tukheit, and Tumatumari (F. E. Lutz); Penal Settlement, Bartica District (W. Beebe); Kartabo and Kalacoon (Wheeler).

Peru: Callanga (Staudinger).

Bolivia: Rio Beni (L. Balzan).

These localities show that *Gigantiops* has a very limited range compared with many Neotropical ants, since it is confined to a strip of South America east of the Andes and extending from about 10° north to 10° south of the equator.[1]

Gigantiops (Fig. 1) is a common ant in the forested portions of British Guiana, preferring shady places rather free from undergrowth and spending most of its time on the ground, running over the dead leaves. It occurs singly, as stated by previous observers, and really belongs to a forest-floor ant-fauna comprising also *Neoponera apicalis* Latr., *obscuricornis* Emery and *commutata* Roger, *Mesoponera constricta* Mayr, *Pachycondyla crassinoda* Latreille and *harpax* Fabr., *Paraponera clavata* Fabr., and *Ectatomma quadridens* Fabr. Those who are interested in mimicry will observe that in its form, the dull black color of its body and yellow antennal tips, *Gigantiops* bears such a striking resemblance to *N. apicalis* and *obscuricornis* that the latter might be regarded as

[1] I find a note by von Motschulsky in a letter published in his "Études Entomologiques" (1855) and referred to in the "Stettiner Entomologische Zeitung" (1859), which seems to apply to *Gigantiops*. Speaking of the insects which he observed at Obispo, Panama, he says: "I observed a lot of ants of diverse and bizarre form, among others one bearing the closest resemblance to a spider, especially to a *Salticus*, and as it also has the ability to leap, I have named it *Salticomorpha nigra*." There are two objections to accepting the name *Salticomorpha* as antedating *Gigantiops:* first, there is no record of this insect's having been taken in Central America or even in Colombia, and second, von Motschulsky may have seen a *Pseudomyrma gracilis* Fabr., which resembles a black Attid spider in form and color, and have mistaken its erratic movements for leaps. The well-known arachnologist, E. Simon (in Emery, "Voyage de M. E. Simon" (Dec., 1887–Avril, 1888). Formicides, Ann. Soc. Ent. France 1890, p. 65 *nota)* noticed that "all the species of the genus *Pseudomyrma* reproduce exactly the forms and colors of the spiders of the genus *Simonella* Peckh. (Attidæ) and the resemblance is equally striking in their gait." For the present it seems advisable, therefore, either to treat *Salticomorpha nigra* Motsch, as a *nomen nudum* or to include it with a query in the synonymy of *Gigantiops destructor* Fabr.

its models. Furthermore, these Ponerines sting very severely, whereas *Gigantiops* can be picked up with impunity. In Kartabo, nevertheless, the models are much less frequently seen than the mimic. This is interesting in connection with the observations of Mr. Tee Van, who finds that in the same region many of the

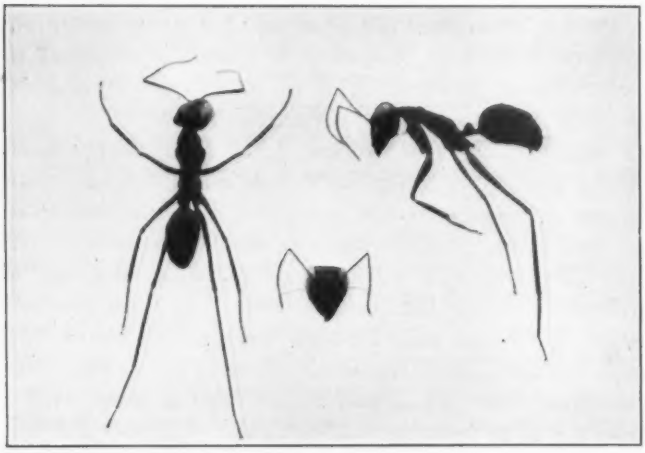

FIG. 1. *Gigantiops destructor* Fabr. Worker, about twice natural size; dorsal and lateral views and head from above.

mimetic butterflies are much more abundant than their putative Heliconid models. It would be a mistake to suppose that *Gigantiops* acts as if it derived any benefit from its striking resemblance to the stinging Ponerines. It greatly surpasses them in agility and when pursued will even leap several inches in a very graceful, cat-like manner. On the rather infrequent occasions when it climbs onto bushes and is running over their foliage it will, if disturbed, leap, without the slightest hesitation, to another leaf or even to the ground and make off with great alacrity. When two *Gigantiops* happen to meet face to face, they exhibit a peculiar play. After stroking each other's heads for a moment with the yellow tips of their antennæ, they move from side to side, precisely like two persons who meet on the sidewalk and try to prevent each other from passing.

On rare occasions *Gigantiops* may be seen carrying a termite worker or other small insect in its jaws, but even such individuals are not easily followed to their nests. Forel's placing of this ant in his tribe Œcophyllini, *i.e.*, with *Œcophylla smaragdina* Fabr., the well-known tree-ant of the Old World tropics, naturally led me to suppose that the nest must be in the trees, but this supposition, which has probably been shared by other myrmecologists, proves to be erroneous. On July 14, after much careful search and persistent following of single workers, my son Ralph succeeded in finding a nest in a partly decayed log only three or four inches in diameter lying on the ground at the edge of the Puruni trail and brought the portion inhabited by the ants into the laboratory. As soon as I began to dig into their nest the workers leaped out and made off, holding their larvæ in their mandibles. The colony comprised only fifty or sixty workers, which had been living in some large cavities made by *Passalus* or other wood-inhabiting beetles. In one of the chambers there were empty cocoons, showing that the pupæ of *Gigantiops* are not nude as in *Œcophylla*, its supposed nearest ally among the Formicinæ. I failed to secure the queen and believe she must have escaped unobserved among the workers. From these she differs merely in her somewhat larger size and slightly more voluminous thorax.

Notwithstanding careful search by my son and myself, ten days elapsed before I could again observe a *Gigantiops* nest. I found the second nest in a similar situation, in a partly decayed piece of a *Cecropia* trunk about a foot and a half long and three inches in diameter, lying loosely on the dead leaves in the shade of a bush. I noticed one of the workers timidly guarding a small hole and hastily retreating into it on my approach. The hole was plugged with cotton and the log carried back to the laboratory. In order that the ants might not elude me as on the previous occasion, I opened the log over a pail of water, but notwithstanding these precautions a few of the workers managed to escape. The entire colony, which was inhabiting one of the large internodal cavities so peculiar to *Cecropia*, was scarcely larger than the former colony, but contained more larvæ and several freshly spun worker cocoons.

No males were present and future attempts to find them and other colonies were unsuccessful.[1]

Two matters call for further discussion in connection with the foregoing observations, the taxonomic affinities of *Gigantiops destructor* and its *modus saltandi*. The generally accepted view of its taxonomic position can be traced to the various papers which Forel has published from time to time on the classification of the subfamily Formicinæ (=Camponotinæ Forel). In 1878 he placed the genus *Gigantiops* between *Opisthopsis* and *Œcophylla* in his first tribe of the subfamily. In his classification of 1893 he omitted all mention of *Gigantiops*, though he enumerated the various other genera of the subfamily. In 1912 he remodeled the classification and considerably augmented the number of tribes, to one of which, the Œcophyllini, he assigned the three genera *Gigantiops, Myrmecorhynchus*, and *Œcophylla*. The same arrangement is preserved in his paper of 1917. I endeavored to show in the same year that *Myrmecorhynchus* could not be retained among the Œcophyllini, but should probably constitute an independent tribe, the Myrmecorhynchini. The characters of the Œcophyllini, according to Forel, are the following: gizzard long and narrow, with straight calyx; clypeal fossa more or less distinct from the antennary fossa; antennæ inserted a little behind the frontal area, but near the anterior ends of the frontal carinæ. The gizzard characters are not peculiar to this tribe, but recur also in the Camponotini, and the remaining characters are decidedly weak, since they depend on slight differences in the proportions of the anterior portions of the head. When we compare *Gigantiops* with *Œcophylla* we are struck by the great differences in the structure of the larva, pupa and adult and in habits. That the habits of the two ants are totally different will be seen from a comparison of the observations above recorded with what we know of *Œcophylla*, and its various subspecies and varieties, which are arboreal ants inhabiting peculiar nests made of leaves and silk spun by their larvæ. Still it may be objected that such ethological peculiarities have little significance, since we have species of *Camponotus* that

[1] Dr. W. M. Mann, who has just returned with the Mulford Expedition from Bolivia, informs me that he found *Gigantiops* nesting under stones in the forests of the Rio Beni.

live in similar nests (*C. senex* Smith and *formiciformis* Forel) and others that live in the ground or in rotten logs (*C. maculatus* Fabr. and *herculeanus* DeGeer). Turning to morphological characters, which the taxonomist regards as much more reliable, we find that the only resemblances between *Gigantiops* and *Œcophylla* (apart from the shape of the gizzard which both share with *Camponotus*) are the shape of the clypeus, with its great, projecting lobe, the shape of the mandibles, and the feeble characters cited by Forel. There are great differences in the size of the eyes and claws, in the shape of the thorax and petiole of the worker, and in the size and shape of the thorax of the female, though the venation of the wings is similar. The larva of *Gigantiops* is like that of *Camponotus*, but very different from that of *Œcophylla*, and the pupa is inclosed in a cocoon. Probably the male *Gigantiops* will be found to exhibit some peculiar differences. Emery (*in litt.*) calls my attention to the singular fact that the tarsal claws of the male *Œcophylla* are almost completely atrophied. It would therefore be very interesting to know the condition of these organs in the corresponding sex of *Gigantiops*. The foregoing considerations seem to me to render it advisable to remove *Gigantiops* from Forel's tribe Œcophyllini and to provide an independent tribe for its accommodation. I find that Ashmead in 1905 had created such a tribe "Gigantiopini," though he included it in a subfamily Gesomyrmicinæ, with *Gesomyrmex* and *Myrmoteras*, genera which, in my opinion, are only remotely related to *Gigantiops*.

It is practically certain that *Gigantiops* is one of a number of ancient, large-eyed, active Formicinæ, once of very wide distribution, but now narrowly confined to the tropics. This group, which embraces also the genera *Œcophylla, Dimorphomyrmex, Gesomyrmex, Opisthopsis, Santschiella,* and *Myrmoteras,* represents merely the surviving specialized tips of diverging branches of a primitive stock. In regard to *Œcophylla, Gesomyrmex,* and *Dimorphomyrmex,* we are actually in possession of considerable paleontological information. Mayr ('68), Emery ('05), and I ('14) have recorded the occurrence of two species of each of these three genera in the Baltic amber, of Lower Oligocene age; Emery ('91) has recorded an *Œcophylla* and a species allied to *Gesomyrmex* (*Sicelomyrmex* Wheeler) from the Sicilian amber, which is

referred to the Middle Miocene; Förster ('91) a species of *Œcophylla* from the Middle Oligocene of Alsace, and Heer ('49) and Mayr ('67) two species from the Lower Miocene of Croatia.[1] More recently Cockerell ('20) described a species of this genus from the Eocene of England, and he ('15) and Donisthorpe ('20) three species from the Middle Oligocene of the same country. The one, or possibly two, extant species of *Œcophylla* are now confined to the hottest portions of the Ethiopian, Indo-malayan, and Papuan Regions. Similarly the few extant species of *Gesomyrmex* and *Dimorphomyrmex* are known to occur only in Borneo and the Philippines.[2] In the same regions and in Burma we find the four species of *Myrmoteras*. *Santschiella* is known only from a single specimen taken in the Belgian Congo, the species of the genus *Opisthopsis* are confined to the Australian and Papuan Regions, and the Neotropical Region possesses only one of these ancient large-eyed Formicines, *Gigantiops*. This, as we have seen, has a rather limited range and is in all probability a true tropical relict, originally developed in and since mainly confined to that portion of the ancient South American continent known as Archiguiana. All of the genera above mentioned are forest ants and most of them are arboreal, but, as we have seen, *Gigantiops* spends most of its time on the forest floor and nests in small, partly decayed logs. *Opisthopsis* nests under bark, in the ground or in earthen termitaria, and I may add that Dr. F. X. Williams, who took the types of *Myrmoteras williamsi* Wheeler in the Philippines, informs me that this ant nests in the soil. From what we know, therefore, of the living and extinct forms, we are justified in concluding that the large-eyed Formicinæ originated during the early Tertiary, or more probably during the Cretaceous, and that the extant forms have since undergone little or no modification, owing to the very stable ecological conditions in which they were able to survive. *Gigantiops*, in particular, may

[1] Since the completion of this paper Professor Cockerell ('21) has described a peculiar large-eyed ant from the Green River Eocene of Wyoming as *Eoformica eocenica*. It seems to belong to the subfamily Fomicinæ and resembles the Australian *Opisthopsis* in the shape of the head and the position of the prominent eyes.

[2] Since this paper was written I have published the description of a *Gesomyrmex* (*G. howardi*) from China.

be said to have an even more remote origin than the archaic though highly specialized Neotropical vertebrates, such as the opossums, manatees, sloths, armadillos, ant-eaters and tapirs among mammals, or the ostriches and hoatzins among birds.

The jumping or leaping habits of *Gigantiops* are so unusual that a more general account of this behavior as it occurs in various Formicidæ may not be out of place. There are two very different kinds of leaping ants, one which I shall call "retrosalient," which always leaps backward, and one that may be called "prosalient," because it always leaps forward. Some authors regard the former as not "leaping," in the proper sense of the term, probably because of the direction and because it is not performed by means of the legs. But such very abrupt displacements of the body are effected in so many different ways in different insects, as, *e.g.*, in Elaterid beetles, Lepismids, Collembolans, cheese-maggots, fruit fly and *Vermileo* larvæ, the extraordinary Coleopteran (?) cocoons described by Berlese ('20, p. 631), etc., that such words as "leaping" can hardly be avoided without pedantry. We even speak of fish or of a cataract "leaping."

Retrosalience has been repeatedly observed in two quite unrelated groups of ants, one embracing the Ponerine genera *Odontomachus* and *Anochetus*, the other the Myrmicine genus *Strumigenys*. By convergence both of these groups have developed very similar long, straight, and linear mandibles, inserted close together on the front of the head and furnished with large, abruptly incurved teeth at their tips. When excited these ants open their mandibles so widely that they stand out at right angles to the long axis of the head or are even directed slightly backwards. And if one of the insects comes in contact with a solid object in its path, it closes them so suddenly and with such force that they make an audible "click" and the insect is thrown backwards through the air to a distance of several inches. I have described this behavior in detail in *O. clarus* of Texas ('00). It has also been observed in *O. chelifer* of Brazil by Schupp (Wasmann, '92) and in the common tropicopolitan *O. hæmatoda* by Nietner ('58), Ferguson (Wroughton, '92), Forel, myself, and others.[1] The method of

[1] Borgmeier ('20) has recently described the similar habits of *O. affinis* in Brazil. "They strike their mandibles against the solid substratum and at the same moment leap 30 to 35 cm. vertically into the air."

leaping in *Anochetus* is precisely similar, as shown by the observations of Wroughton ('92) on *A. sedillotii* var. *indicus* of India, and of Biró (Emery, '97) on a Papuan species. Among the Dacetonini it has been observed by Hetschko in the Brazilian *Strumigenys saliens* (Mayr, '93) and by Biró ('97) in *S. chyzeri* Emery ('97) of New Guinea. The worker of the latter species is able to leap backward to a distance of 20–25 cm., or about 100 to 150 times the length of its body, but this behavior is not exhibited by the female. Forel ('93) believed that the Neotropical *Acanthognathus ocellatus* Mayr and *Daceton armigerum* Latr. might be able to leap in the same manner. I have failed to observe the habit in the allied Australian ants of the genus *Orectognathus*. All the retrosalient ants, however, leap rather reluctantly and only under certain conditions, and the length of their leaps varies directly as the degree of solidity of the objects against which they happen to close their mandibles.

Prosalience is exhibited by at least three very different groups of ants: certain bull-dog ants of the Australian genus *Myrmecia*, *Gigantiops*, and the extraordinary genus *Harpegnathos*, or *Drepanognathus*, as it was formerly designated, of the Indomalayan Region.

The leaping Myrmecias, popularly known as "jumpers" in Australia, comprise the members of Emery's subgenus *Pristomyrmecia* (*fulvipes* Rog., *mandibularis* Sm., and *piliventris* Sm.) and the smaller species of *Myrmecia* sens. str. allied to *nigrocincta* Sm. and *pilosula* Sm. I have frequently seen these ants jump distances varying from one to a few inches. When disturbed *M. nigrocincta* and *pilosula*, especially, present a ludicrous appearance as they bound out of their small mound nests in a series of short hops like Lilliputian cavalry galloping to battle. Examination of these ants reveals a structural peculiarity which has been overlooked by previous observers, namely, a distinct elongation and basal incrassation of their hind femora, as compared with the hind femora of the other nonsalient species of the genus. In Fig. 2 the hind femur of a worker *M. nigrocincta* (*c*) and that of a small worker of *M. sanguinea* of the same size (*d*) are drawn to the same scale. The greater length and volume of the femur of the former species shows a distinct approach to the conditions in the

saltatory Orthoptera and is evidently to be interpreted as an arrangement for the accommodation of a more voluminous and therefore more efficient extensor, or abductor muscle in the hind leg. This morphological peculiarity, together with the leaping habit, seem to me to be sufficient to justify a separation of these jumping species from the remaining Myrmecias as a distinct subgenus, for

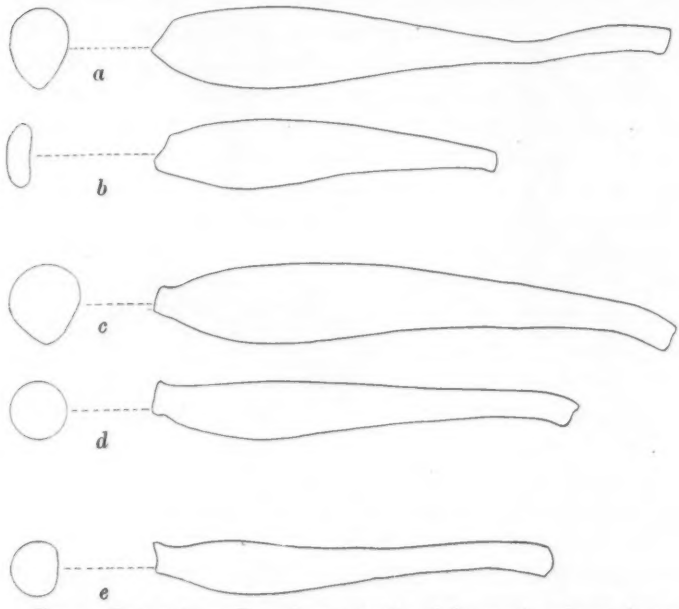

FIG. 2. Femora in profile and cross section of five species of ants drawn to the same scale. *a, Gigantiops destructor; b, Componotus castaneus americanus* Mayr; *c, Myrmecia nigrocincta* Smith; *d,* small *Myrmecia sanguinea* Smith; *e, Harpegnathos saltator* Jerdon.

which the name **Halmamyrmecia** subgen. nov. (with *pilosula* F. Smith as subgenotype) may be proposed.

In *Gigantiops* I find an even more pronounced elongation and basal incrassation of the hind femur than in *Pristomyrmecia* or *Halmamyrmecia.* As there is only one species of *Gigantiops,* I have compared its hind femur (Fig. 2*a*) with that of a non-leaping *Camponotus* worker of the same size (*b*). It will be seen that the difference in the length of the two femora is very pronounced,

but that the difference in the basal incrassation is not so striking when the parts are seen from the side. The shapes of the cross-sections of the bases of the two femora, nevertheless, show that the *Gigantiops* femur is much more voluminous and therefore capable of furnishing attachment for a much larger and more powerful extensor muscle, as in the crickets and grasshoppers.

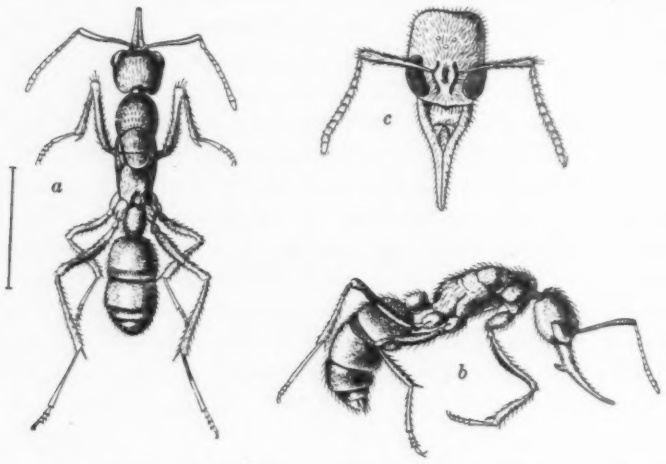

FIG. 3. Female of *Harpegnathos saltator* Jerdon (after Mayr.). *a*, dorsal view; *b*, lateral view; *c*, head of same from above.

Extraordinary feats of leaping are performed by the species of *Harpegnathos,* a genus confined to Indochina and the Philippines. In these ants (Fig. 3) the structure of the head is very singular, the eyes being very large, larger, in fact, than in any other Ponerine, and placed very far forward, and the mandibles are quite unlike those of any other known species. They are very long, separated at the base but approximated, arcuately curved upward, and gradually tapering toward their tips and finely serrate along their inner borders. Each is provided at the base with a large, flat, triangular tooth, projecting inward and somewhat downward and backward. In cabinet specimens the blades of the mandibles are applied to one another and the basal teeth overlap. The leaping habits of this insect have been observed by Lefèvre,

Lewis ('82), Wroughton ('92), and Bingham ('03). Lefèvre states that it can make leaps of 20 to 25 cm., and Lewis saw it rise into the air to a height of 5 or 6 inches till exhausted, when its leap did not exceed an inch. Wroughton says: "The single specimen of the genus, which I have had the luck to find, made leaps of a foot or 18 inches with perfect ease, exactly like a grasshopper. I had much trouble in securing this specimen, and, when I succeeded, I found she could sting better than she could leap." Unfortunately we have no observations on the *modus saltandi* of this curious insect. Its hind legs are really very short and even thinner than those of many nonsalient ants as indicated in the figure of the hind femur of a worker *H. saltator* Jerdon (Fig. 2*e*). As this ant is nearly of the same size as the specimens selected for the other femora (*a–d*), and as the outline is drawn to the same scale, it will be evident that no such feats of leaping as described by Wroughton can be performed with such appendages. We must conclude, therefore, that the mandibles are employed for this purpose, but how they function is a matter of pure conjecture till the living insect can be carefully studied. It is conceivable that when about to leap the *Harpegnathos* opens her mandibles slightly till the two basal teeth just barely touch, and that she presses the tips of the mandibles against the ground so that their long, slender, and probably very elastic blades are more arcuately bent. We may suppose, moreover, that if the two teeth are suddenly permitted to slide over each other, with a concomitant sudden unbending of the mandibles, the insect would be precipitated forward much like a very elastic strip of metal or whalebone bent in an arc and suddenly released. It is less probable that the insect leaps by inserting the tips of the mandibles in the ground and bending them in the opposite direction, *i.e.*, by more nearly straightening them and then suddenly allowing them to return to their original curvature.[1]

[1] Since this paragraph was written I find that Professor Forel (1921, p. 47) gives some notes on the method of leaping employed by *Harpegnathos*. He states, apparently on the authority of some correspondent in India or China, that this ant "fait des bonds formidables de plus d'un mètre à l'aide de ses longues mandibules un peu recourbées en haut. La tête entière se recourbe sous le corps, se rejettant ensuite en avant, un peu à la manière du thorax de nos insectes d'Europe nommés taupins."

In conclusion, two interesting matters of a more speculative nature may be briefly discussed:

1. The various macrophthalmic, or large-eyed, tropical ants mentioned in this paper, namely, the Formicine genera *Gigantiops, Opisthopsis, Œcophylla, Gesomyrmex, Dimorphomyrmex, Santschiella* and *Myrmoteras,* the Ponerine genera *Myrmecia* and *Harpegnathos,* and I may add also the whole subfamily Pseudomyrminæ, constitute only a small percentage of the more than 10,000 extant species, subspecies, and varieties of Formicidæ. In the great majority of forms the eyes and ocelli of the female, and especially of the workers, have undergone considerable reduction in size or have entirely disappeared. In the male, however, which is the more conservative sex in ants, the eyes and ocelli are always large. These facts, together with what is now known of the ants of the Baltic amber, suggest that not later than Cretaceous time the females and workers were also all large-eyed, like the Scoliidoid wasps from which the Formicidæ are derived, and that they preserved this condition till after the social habit and a wingless worker caste had been evolved. During the Eocene and owing to the further development of the peculiar nesting and foraging habits, the females and workers became increasingly microphthalmic and anophthalmic till the small-eyed or blind condition became established in the majority of existing forms.

2. It will have been noticed that all the known prosalient ants have very large, convex, and minutely faceted eyes, and that all belong to archaic genera. I have already discussed the antiquity of *Gigantiops.* The Myrmecias are, I believe, justly regarded as the most primitive of existing ants, survivors, without more than specific diversification, from the early Eocene or the late Cretaceous. *Harpegnathos* includes only a few rare species of very restricted geographical range, evidently relicts on the verge of extinction. It would seem, therefore, that the leaping habit may have been much more general among the most ancient macrophthalmic Formicidæ, but had been abandoned as incompatible with a more highly developed social organization. This seems to be shown even within the genus *Myrmecia,* the larger and more dominant species of which no longer leap. That this habit should still persist, probably in a degenerate stage, in a few large-eyed forms,

may be due to the fact that ants endowed with unusual visual powers can retain such a habit with some impunity. Santschi ('11) and Brun ('14) have shown that vision is an essential factor in the homing behavior of ants that do not adhere very strictly to the topochemical trail made by themselves or their fellows from and to the nest. The leaping habit, if preserved and assiduously practiced in small-eyed ants, would, of course, often render it difficult or impossible to find the nest by means of the antennal sense alone.[1]

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[1] The mollusks of the genus *Pecten* are interesting in this connection, since, as is well known, they are able to leap considerable distances through the water by rapidly opening and closing the valves of the shell and have their mantle margins beset with large, highly specialized eyes.

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THE RELATION OF THE MADREPORITE TO THE PHYSIOLOGICAL ANTERIOR END IN THE TWENTY-RAYED STARFISH, PYCNOPODIA HELIANTHOIDES (STIMPSON).*

H. P. KJERSCHOW-AGERSBORG.

TEN FIGURES IN THE TEXT.

In a previous paper ('18) the writer recorded some facts concerning the bilateral tendencies and habits in *Pycnopodia helianthoides*. These were based on data gained from experimental studies and on others from observations on the behavior of the organism in its native environment. It was the writer's purpose at that time to follow the paper of 1918 with one on the physiology and histology, as well as other structural features of this species, and for this reason certain points were omitted from the paper mentioned above which might well have been included therein. Owing, however, to the writer's remoteness from the Pacific coast for the last five years and the lack of material on which to conclude this second work, it has been quite impossible for this additional contribution to appear sooner. During the last summer (1921) the writer was, however, so fortunate as to find opportunity to visit Puget Sound and gather some additional information on *Pycnopodia*. (It may be of interest to note in this connection that the transplantation of *Pycnopodia* from Bremerton to West Seattle was successful, which was shown by the fact that specimens of various sizes were found on September 2, 1921, on the piles under the docks at West Seattle, where about 12 specimens were planted in the spring of 1915, notwithstanding the difference in salinity at these two places. It was impossible, on account of lack of time, to determine whether the specimens found at West Seattle, 1921, were the same as those planted there in 1915, or whether they were the progeny of the latter. *Vide* Kjerschow-Agersborg, 1918.) From the additional data gathered this summer (1921) it is possi-

* Contributions from the Zoölogical Laboratory of the University of Illinois, No. 197.

ble to conclude this paper, although in an abridged form.

Investigators do not agree in regard to the position of the madreporic plate in Asteroidea. Ludwig ('99), dealing with the genus *Asterias,* says:

"Falls wie es, trotz der nicht seltenen Ausnahmen die Regel ist, nur eine einzige Madreporenplatte vorhanden ist, liegt sie stets im vorderen linken interradius, wenn man den Seesterne bei abwärts gerichtetem Munde mit dem Interradius des Afters nach vorn stellt," p. 540.

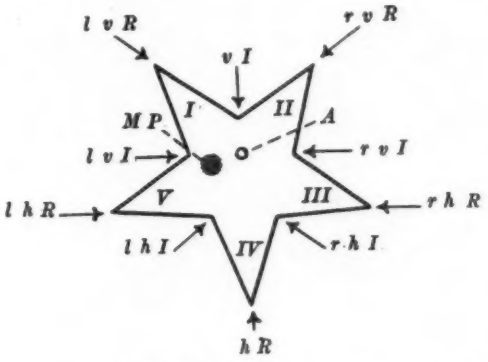

FIG. 1. A copy of Ludwig's figure of the asteroid groundplan, showing Ludwig's morphological "anterior" end. (P. 537.)

A, anus; *h.R*, posterior radius; *l.h.I*, left posterior interradius; *l.h.R*, left posterior radius; *l.v.I*, left anterior interradius; *l.v.R*, left anterior radius; *M.P*, madreporic plate; *r.h.I*, right posterior interradius; *r.h.R*, right posterior radius; *r.v.I*, right anterior interradius; *r.v.R*, right anterior radius; *v.I*, anterior interradius.

Agassiz ('77) claims that the madreporite is always in the suture of the terminal arm of the pentagon, which brings it opposite the third arm. This is also the view of Bury ('95). Rathbun ('87) says it is generally placed about midway between the center and the margin of the disk, and Sedgwick ('09) records that the madreporite varies in number in various species of starfish.

Delage and Hérouard ('03) say: "Elle est située dans la région apicale, tout près de la centro-dorsale, dans un interradius autre que celui qui porte l'anus. Le madréporite détermine une deuxième symétrie bilatérale, mais qui est altérée par l'anus, comme celle

qui dépends de l'anus est altérée par le madréporite.

"Quand on regarde l'animal par la face dorsale, l'interradius madréporique vient après l'interradius anal, séparé de lui, d'un côté, dans le sens indirect (inverse de celui de la succession des heures sur un cadran), par un seul interradius, de l'autre par deux interradius," p. 2.

". . . quand on regarde l'animal par le pôle apical, l'anus est en arrière, le madréporite en avant et à droit," p. 3.

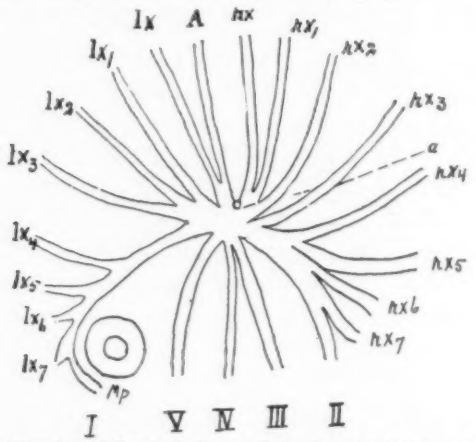

FIG. 2. Ritter's and Crocker's figure of the dorsal radial muscles of *Pycnopodia helianthoides*, showing the relation of the radial muscles to the asteroid groundplan, as represented in Fig. 1. *A*, the "anterior" ray; I-V, the "posterior" rays; rx–rx_7, rays added, on the right side, to the original six rays after metamorphosis; lx–lx_7, rays added to the left side; *a*, anus; *Mp*, madreporite.

Shipley ('93), MacBride ('96), and Lankester ('00) do not commit themselves in regard to the position of the madreporite, *i.e.*, as far as the starfish is concerned.

Ritter and Crocker ('00) in their work on *Pycnopodia* adopted Ludwig's and Agassiz's plan of numbering the radii of the typical five-rayed echinoderm. According to this, when the apical side is uppermost, counting from the madreporite clockwise, the rays are numbered from I.–V. These authors go on by saying: "From a study of the metamorphosis, Ludwig, '82, considers that the star should be oriented by a line running interradially between I. and II. and radially along IV., thus bringing the madreporite in the left anterior interradius" (Fig. 1).

"Before Ludwig was consulted, this orientation had been adopted for *Pycnopodia,* owing to the striking bilateral symmetry displayed in the young animals. This symmetry determined that the sixth ray is median anterior between I. and II., and by us has been called "*A*" (Figs. 4, 5). Ritter and Crocker's diagram (Figs. 4 and 5) agree with Ludwig's (Fig. 1). The relative position of ray "*A*,"

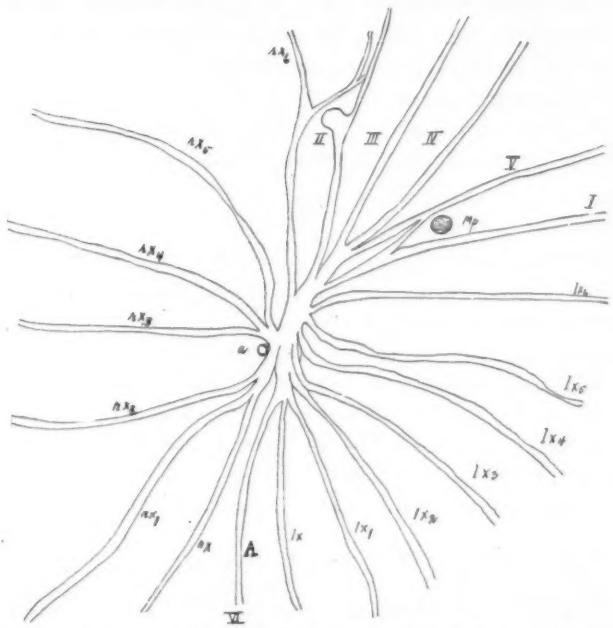

FIG. 3. A diagram of the dorsal radial muscles of *Pyncnopodia helianthoides* to show the relation of the primary and secondary rays to the physiological anterior end. (Rays I, lx_0, lx_5, lx_4, lx_3, correspond to I, V, IV, III, II (Fig. 2) respectively); rays I–V, rays of the physiological anterior end; these rays, and ray *A*, are, perhaps, the primary rays; rays lx–lx_0, the secondary rays of the left side; rx–rx_0, the secondary rays of the right side correspondingly; rays rx_0, and lx_0, the youngest rays. *a*, anus; *Mp*, madreporic plate. This sketch is made from the under side of the dorsal muscles.

in *Pycnopodia,* according to Ritter and Crocker, to the five rays of the asteroid ground plan, is between the left and right anterior rays (Figs. 1, I.–II.; and 4, I.–II.); the axis of bilateral symmetry, or Ludwig's orientation line, lies along rays *A*–IV. (Fig.

4), or along a line drawn between vorderer Interradius-hinterer Radius (Fig. 1).

Delage and Hérouard claim that the relation of the madreporite is far from being precise, and their orientation of the asteroid plan corresponds to Ritter and Crocker's figures of young individuals, if they be inverted. This is true, however, only in a general sense for the madreporite which comes on the right side, but the anus is placed in the same relative position in either case. This relation is different in the adult. Here the madreporite is on the left anterior side between the rays I. and V. and actually corresponds to Ludwig's plan. But the so-called five primary rays of Ritter and Crocker, which, according to Ludwig ('99), correspond to 3–IV.,

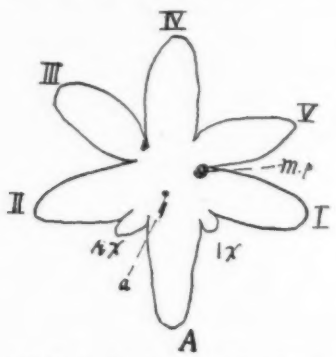

FIG. 4. Young individual, aboral view, in the eight-rayed stage (from Ritter and Crocker); the sketch is inverted to show the probably anterior rays (I–V) and their relation to the madreporite and the anus, *mp*, *a*, respectively. *A*, the posterior primary ray. (Compare this figure with Figs. 6, 7, 8, 9). The labeling is retained as in the original.

2–III., 1–II., 5–I., 4–V., respectively (Fig. 6), for the larva and the ground-plan of the common starfish, are not the posterior rays in adult life of *Pycnopodia*, however, but the anterior rays. This is easily seen in an actively moving individual, and may also be readily learned from the study of the interpolation zones which lie between rays II.–VI., VI.–I. It seems quite reasonable that the movements of *Pycnopodia* should be in the direction of, or along the axis of, the oldest rays, with the oldest rays as determiners of direction of movements. For, as I have shown before ('18), this

starfish does not only move with the same side all the time as anterior end, but its speed is considerably greater than that of the common star; its highest speed, *e.g.*, when moving to deeper water during the receding tide, was 122.5 cms. per minute. Opposite to the largest number of rays, in early post-larval life, is one ray, which is perhaps of the same age as the other primary rays, and with this single ray are young ones, varying in strength and age. As a matter of fact, it should be expected that if there are any distance receptors at all, which act as influencing factors on behavior, they would be present in the earliest developed tentacles. This seems to be probable in *Pycnopodia:* It always moves at right angles to the zones of radial growth; the anterior end in adult life, being always the side which possesses the fewest, but uniformly sized, rays anterior to the radial interpolation zones; *in young specimens the number of the large rays is greater for the anterior end.* In adults the number of the anterior rays is five; and the youngest of all rays is a pair, one on each side of rays II. and I.; the number of rays of the posterior end varies with the total number of rays. In living animals it is quite easy to distinguish between the ages of the rays. There is a gradual increase in size of the rays posteriorward from the interpolation zones, the youngest being, of course, found at the latter points. This seems to indicate that the so-called posterior end is the physiological anterior end.

Kjerschow-Agersborg ('18) demonstrated experimentally that out of 50 righting reactions of *Pycnopodia,* 46 were toward the anterior end with an average speed of about 57.1 sec. per normal turn. In this species a physiological anterior point is actually established (*vide ut supra et infra*), the anterior ray is ray IV.; the madreporite holds the relation as indicated by Ludwig, Agassiz, Ritter, and Crocker for the five-rayed starfish (Figs. 1, 4, 5, 6, 7).

It may be noted that in Ritter and Crocker's diagram (Fig. 2) the anus is in front of the base of the radial muscles, according to the interpretation of these writers; but by the establishment of the physiological anterior end the anus comes nearer the posterior end than before, while the madreporite is placed nearer the anterior end. This, however, does not change their relation to the respective rays, but the relation remains the same as before. That is, the

madreporite is still in the interradius V.–I. of Ludwig. The position of the anus, in fact, corresponds, now, with Delage and Hérouard's asteroid plan. Figure 2 is copied from Ritter and Crocker ('00) and represents a diagram of the muscles of the aboral disk, seen from the inside, and as though looked down upon, showing the apical radial muscle bands, the madreporite, and the position of the anus close to the origin of the muscle of ray *A* (VI.). If ray *A* were the anterior end, then the anus would be anterior to the center of the dorsal side; but since ray *A* is, in fact,

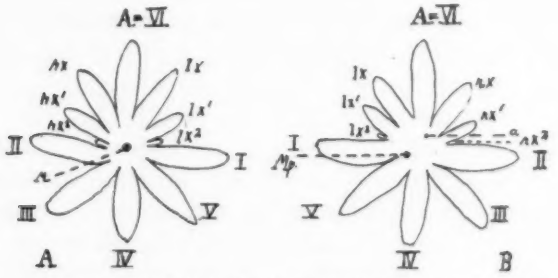

FIG. 5. Young individuals in the 12-rayed stage to show the interpolation zones: rx^2–lx^3. These figures are as per the original and show the reverse condition as in Fig. 4, which has been inverted to show the right relation of the madreporite to the true anterior end. *A*, oral view; *B*, aboral view. (From Ritter and Crocker.)

the posterior ray, the anus becomes placed posterior to the mid-dorsal point. Delage and Hérouard ('03) adopt Cuénot's plan ('91), with the madreporite in the interradius III.–II.; the anus in interradius II.–I., a little posterior of the mid-dorsal, but also a little to the right of the median line (Fig. 9). This seems to be an arbitrary matter of orienting the star. If the interradius I.–II. of Cuénot is placed as anterior end, the anus comes in the similar position as in Ludwig's plan.: the madreporite is in interradius II.–III.; the anterior end is ray III. (Fig. 9). My drawing of the radial aboral muscles does not correspond at all with Ritter and Crocker's, in the point of orientation, and, in fact, also in the points relative to the general radiation of these muscles. I have compared the arrangement of the apical radial muscles in both large and small individuals having the same relative number of rays and

have found them to be exactly as represented in my sketch (Fig. 3). I can not accept Ritter and Crocker's orientation represented in their sketch (Fig. 2); but even if their interpretation should be correct, and indeed it may be for young individuals, *it does not hold for adults relative to their physiological anterior end.* Rays II., III., IV., V., I. represent the anterior end in respect to progressive movements of the starfish in its native environment (Fig. 3). The figure here is inverted, *i.e.,* the madreporite should face the reader on his left side; the sketch is made from the inner side

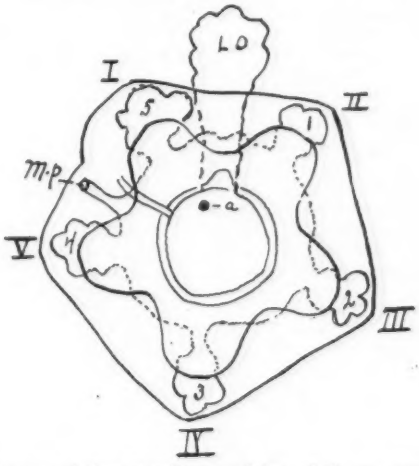

FIG. 6. Diagram of the asteroid groundplan of the metamorphosing common starfish. 1–5, radial vessels (larval); I–V, adult radial vessels; *a*, anus; *Lo*, larval lobe organ; *mp*, madreporite. (From Ritter and Crocker.)

of the aboral disk, looking down upon it. I am not concerned, at this time, about the controversy I may be led into relative to the difference between Ritter and Crocker's diagram and their interpretation and my diagram; I am only recording facts relative to the physiological anterior end in *Pycnopodia helianthoides* (Stimpson), and I am trying to adjust myself as far as possible with the accepted view in this field of morphology. In my opinion, the apical radial muscles of *Pycnopodia,* relative to their axial arrangement to the physiological anterior and posterior ends, fit in very well with the marked bilaterality of the adult, as I have recorded

elsewhere ('18). The radial symmetry is, indeed, superimposed.

Cole ('13) demonstrated with marked clearness, experimentally, what Cuénot and Delage and Hérouard had demonstrated morphologically, viz., that ray III. is the anterior ray. Cole, from his experiments on *Asterias forbesi*, constructs a line of bilateral symmetry with regard to his records; an approximately equal number of trials fall on each side (Fig. 8). A line drawn perpendicular

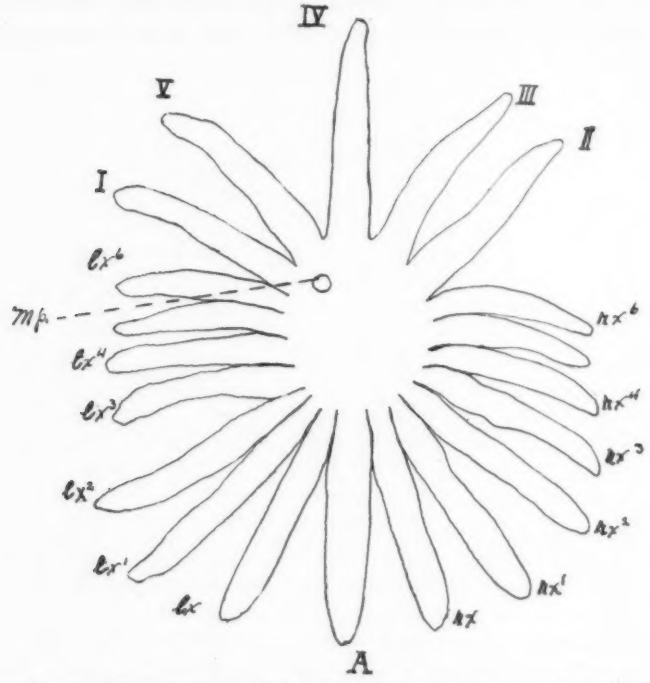

FIG. 7. Diagram of an adult individual of the twenty-rayed starfish to show the bilateral appearance in an individual actively moving about, and the relation of the madreporite (mp,) to the physiological anterior end (rays I–V); and of the anus (a) to the rest of the dorsal disk. *A*, primary posterior ray. rx–rx^6, the oldest and youngest right post-larval rays; lx–lx^6, oldest and youngest left post-larval rays.

to the line of bilateral symmetry, intersecting mid-dorsally, brings out of the total number of 499 trials: 347 ahead of it, *e.g.*, on the side which bears the madreporic plate; 152 behind, or to the side

which bears the anus. Ray IV. records 107 trials, ray III. 137, and ray II. 103 trials out of the total of 499; while rays V. and I. have only 74½ and 77½, respectively. This is, indeed, a very striking contrast to Ludwig's so-called "vorderer Interradius," *e.g.*, interradius I.–II., the *ipso facto* posterior end. If the physiological anterior rays of *Pycnopodia are in fact the morphological anterior rays*, as represented by Ritter and Crocker (although theirs must be inverted), then all facts agree. (Compare Figs. 2, 3, and 7.) In *Pycnopodia* the line of bilateral symmetry lies along

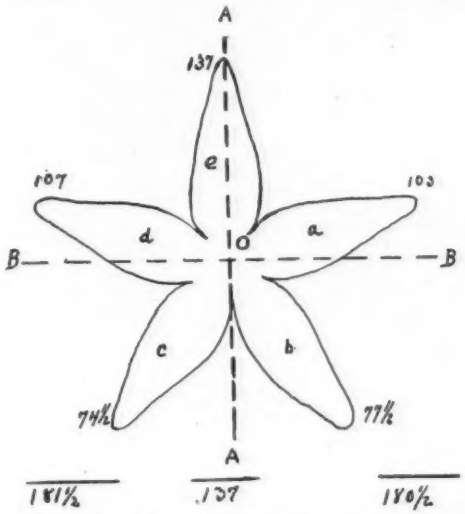

FIG. 8. Diagram to show the physiological anterior end of *Asterias forbesi*, and its relation to the madreporite. Line *AA*, plane of bilateral symmetry; *BB*, dissects the star into an anterior and posterior pole according to direction of locomotion. The *number* at the end of each ray indicates the exact number of attempts the star used that ray as "anterior" ray in locomotion; ray *e*, is seen to have the largest number in its favor. (Ray *e* = III, Cuénot.) The sum of the trials indicates a "right" and "left" which correspond very well to a plan of bilateral symmetry. (From Cole.)

the rays IV.–*A* (ray *A* = VI.); this is explainable by the fact that five of the six primary rays become the anterior rays, with ray IV. in the lead, and rays III., II. on the left, and V., I. on the right (Fig. 7). The relation of the madreporite and of the anus to the dorso-radial muscles is then demonstrated (Figs. 2 and 3). Ray

A (or VI.) is the median posterior ray (Fig. 7), while ray IV. is in the lead. Figs. 4 and 5 show the relation of the madreporite to the physiological anterior end in young specimens of *Pycnopodia;* the apical ray, *e.g.*, ray IV., is uppermost on the page (Fig. 4). In Fig. 5, *A* represents the oral view. Ritter and Crocker accepted as anterior end that pole of the star which corresponds to the larval lobe organ (Fig. 6, *Lo*), but if the physiological anterior end in *Pycnopodia* corresponds to the posterior end of the common starfish, then the larval lobe organ has nothing to do with it, at least not in *Pycnopodia*. It is, of course, an open question whether the anterior rays (II., III., IV., V., I., Fig. 3) correspond to the posterior rays of the same numbers in Ritter and Crocker's sketch (Fig. 2). If they do not, then the physiological anterior end in the adult *Pycnopodia* has become established independently of the factors as noted above. But this may not be the case. Of course,

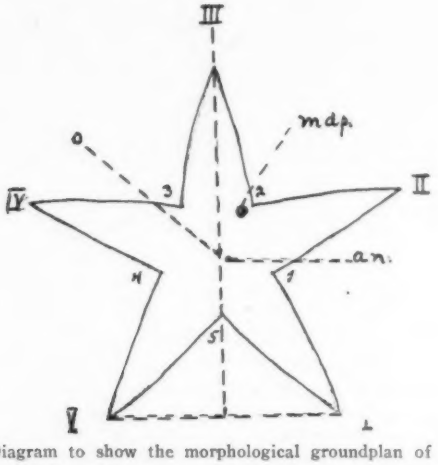

FIG. 9. Diagram to show the morphological groundplan of the common starfish. III, anterior end; *an*, anus; *mdp*, madreporite; *o*, morphological center; 1–5, interradii; I–V, radii. (From Delage and Hérouard.)

the common starfish may indeed move with any of its rays in the lead (Jennings, '07, p. 155); and "do the same thing, under the same conditions, in a number of different ways, and never do the same thing twice in exactly the same way" (Coe, ('12)). The anterior ray of these species of starfish (*Asterias forreri, A. for-*

besi, and *A. vulgaris*) has not been easy to determine in the adult. Although Dr. Cole, as we have seen, comes nearest to establishing an anterior pole in the five-rayed starfish, *A. forbesi* (Fig. 8). Jennings ('07), in experiments on righting reactions, also found that: "Individual starfish do have a more or less permanent 'set' toward the use of a certain ray in pulling themselves over in the

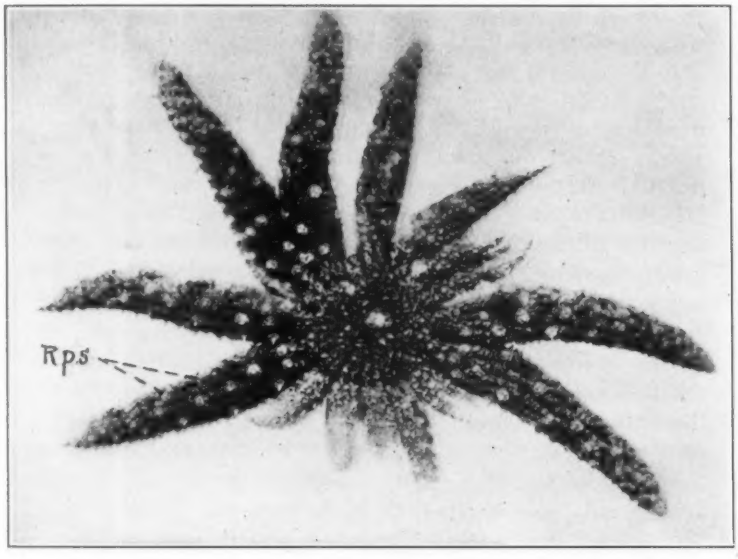

FIG. 10. Photograph of a small specimen of *Pycnopodia helianthoides* with 14 rays. Notice five rays on one side, and two on the opposite side, are regenerating from autotomy. *Rps*, respiratory papillæ. Natural size. Photo by author.

righting reactions." *A. forreri* uses the same ray (*e.g.*, ray *e*, *vide* Fig. 8) that *A. forbesi* uses as anterior pole. This anterior pole seems to be directly homologous with the anterior end in *Pycnopodia*, judging the size of the rays and their relation to the smaller ones in the latter.

The number of madreporites, especially in multiradiate species, may vary: Cuénot ('91), Ludwig ('99), Delage et Hérouard ('03), Sedgwick ('09), Verrill ('14), Crozier ('21), and on that account the true position of the madreporite is difficult to determine. In

a few cases I have found the madreporic plate present on the right anterior nearly opposite the base of ray V., but I have never found more than one in *Pycnopodia helianthoides*. Crozier ('21) records asexual reproduction in *Coscinasterias tenuispina* (Lamk.), its model number of rays in the adult being seven, and that, together with this method of autotomous multiplication, madreporites are also multiplied at separate points on the disk: "an assurance that portions of the body separated by autotomy will each be provided with a madreporite." He abandons the notion which he held at first, that "There is a physiological basis for the development of one or several madreporites according to the number of rays, *i.e.*, depending on the total water requirements of the locomotive organs." *Pycnopodia*, a much larger species (even though the ray lengths in the two species may be the same, *Pycnopodia* is larger in bulk than *Coscinasterias*, because it has about three times more rays than the latter), and with a locomotive speed about nine times greater than *Coscinasterias*, has usually only one madreporite. That is, it gets along with only one. Sometimes autotomy is practiced in *Pycnopodia* (Fig. 10), but not for the purpose as recorded by Crozier for *Coscinasterias*. Verrill ('14) reports a multimadreporic case for *Pycnopodia*, but he considers that to be abnormal. It seems, therefore, that while the anterior end in *Pycnopodia* is much the same as in the common starfish, the position of the madreporite on the dorsal disk may vary. But it is always nearer the physiological anterior end. Crozier also finds this to be true for *Coscinasterias*. The fact that *Pycnopodia* is bilaterally symmetric even after metamorphosis (no one has seen the larva of *Pycnopodia*, but it is assumed that it is bilaterally symmetric as in other echinoderms) may be a factor which aids it in the development of a locomotive speed greater than that of other starfish, and that it consequently "selects," by means of the law of least resistance, the oldest and most efficient pole as anterior end. This pole, judging from the relationship which the smallest rays bear to the physiological anterior end, is at right angles to the two interpolation zones, the zones of the least locomotive efficiency during the postembryonic development. Ludwig's asteroid ground-plan, applied to the ordinary starfish, does not hold completely for the twenty-rayed starfish; his "vorderer Interradius" becomes the "hinterer Interradius." The physiological anterior end corresponds more nearly

to Cole's finding for *Asterias forbesi*, viz., that part in proximity to the madreporite is the anterior physiological end, the madreporite being on the left anterior side.

Summary.

1. The physiological anterior end in *Pycnopodia helianthoides* corresponds to the posterior end of Ludwig's ground plan for *Asterias*. The anterior end possesses a relatively larger number of old (large) rays in early life than it does in late life. The new rays are added at two interpolation zones posterior to rays II., I.

2. The madreporite is, as a rule, on the left anterior side; it varies in position, but it is always found on the anterior part of the dorsal disk, *i.e.*, at the base of rays III., IV., or V. The so-called five primary rays (Ritter and Crocker), which, according to Ludwig, correspond to 3–IV., 2–III., 1–II., 5–I., 4–V., respectively, are not the posterior rays in adult life of *Pycnopodia*, but the anterior rays. Ray IV. is the anterior ray in adult life.

3. The establishment of the physiological anterior end in *Pycnopodia* shows that the madreporic plate is anterior to the mid-dorsal and the anus posterior; this arrangement agrees fairly well with Delage and Hérouard's plan for the five-rayed starfish. It also corresponds with Cuénot's plan for the common starfish, with Jennings's "more or less permanent 'set,'" and with Cole's "physiological anterior"; it is the reverse of Ludwig's asteroid ground-plan relative to the numbering of the rays.

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